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dealing with Race and Inheritance in the Fields of
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DEMOGRAPHY AND ANTHROPO-GEOGRAPHY

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THE MANKIND QUARTERLY

— mala opinio bene parta delectet —

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The late A. M. Ludovici's Bequest to the University of Edinburgh

By R. GAYRE OF GAYRE

The late Mr A. M. Ludovici was well known as a political philosopher, and with that aspect of his work we have nothing to do; or have we anything to say on the subject of the question of his religious, or lack of religious, views. But there are certain aspects of his bequest to Edinburgh University which are material and which we are bound to comment upon.

First of all, however, we may give the following outline of the career of the late Mr A. M. Ludovici for the interest of our readers.

He was born in France, the son of a well-known painter, in which medium he also worked very well. He joined the army and went to France with the B.E.F. in 1914 and served in the artillery in the battle of the Somme. When the War Office discovered that he spoke both French and German fluently he was sent to translate official documents at the War Office. From about 1919 onwards he occupied himself writing. The fields of historical subjects, sociology and heredity, as well as various novels, he made his own. His well-known books were biographical and they included *Nietzsche* (1919) and *Auguste Rodin* (1926). He had been private secretary to Rodin in 1906.

He was a very strong writer upon miscegenation, and devoted part of his life to this topic, which brings us to the facts which we are to reveal in this short paper.

In 1971 his will was proved in the High Court of Justice. In this will, after sundry bequests, he goes on to bequeath:

> . . . I direct my Trustees to stand possessed of the residue of my Residuary Estate in trust for the University Court of the University of Edinburgh Incorporated under the Universities (Scotland) Act 1899 to be held in trust by the said University Court for the following purposes, namely:
>
> (c) As to the sum of £2,000 to be invested in trustee securities and the income thereof to be used to provide a money prize to be known as "The Ludovici Prize" to be awarded annually or at the discretion of the said University Court for the best thesis submitted to them on the subject of miscegenation.
>
> (d) With regard to the balance of the said residue of my Residuary Estate I direct the said University Court to use the same at their discretion for the purpose of research into the influence of miscegenation on man's quality and well-being,

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such research to be carried out under the auspices of the University Department of Public Health and Social Medicine.

The purpose of the research is quite clear, and the ends to be achieved are not trammelled in any way by judging what they will be. It is placed under the University and under its department of Public Health and Social Medicine to guarantee that it is of the highest quality.

To this the University of Edinburgh replied as follows:

I again refer to your letter of 7th April. The question of being able to implement the terms of the Ludovici bequest has now been considered most carefully by our Faculty of Medicine which has approved the enclosed document on the subject prepared by the Professor of Social Medicine.

I am now asked to put to you and the Executors the proposals contained in the document to see whether, in your view and theirs, our proposals would be in compliance with testamentary wishes. It should be pointed out that this, in the opinion of the Faculty, is the only way it could make use of the bequest.

The document which the University enclosed from Professor S. L. Morrison, Department of Social Medicine at the Usher Institute, Warrender Park Road, Edinburgh, and dated 21st April 1972, reads as follows:

LUDOVICI BEQUEST

Under the terms of the Ludovici will the Court is "directed" to use the major part of the bequest "for the purpose of research into the influence of miscegenation on man's quality and well-being, to be carried out under the auspices of the University Department of Public Health and Social Medicine." A dictionary meaning of miscegenation is: a mixture of races, especially of white and negro races, and the meaning of race is a group of persons or animals or plants connected by common descent.

No doubt it would be very interesting and useful to study the influence of mixture of white and negro race on man's quality and well-being, but the Department of Social Medicine is not at present geared to such a study and Edinburgh would not be a suitable place to carry it out. From figures supplied by Professor Emery it appears that there are only a few hundred coloured persons in Edinburgh and the amount of marriage between them and white Edinburgh people is so small that to study more than a few dozen of families one would have to go well beyond the bounds of Edinburgh. Moreover, such a study would be a very delicate matter to embark upon.

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It would be difficult to ascertain the families one would be interested in, and, having ascertained them, enquiries about the exact race status of the marriage and the offspring might well stir up feelings of resentment against the researcher, the Faculty and the University.

It would seem to be more satisfactory from the point of view of all concerned if we would make our research deal with an aspect of race which the Department is better equipped to deal with and which would bring credit rather than misunderstanding to the University. A race is a group of people united by common descent. The Department is at present engaged in a research of such a group. We are interested in those people who are suffering from Huntington's chorea and the influence of their marriage on the quality and well-being of their offspring and the total effects of such marriages on society as a whole. Huntington's chorea is a chronic neurological condition which starts on average in the middle thirties. Choreiform movements are progressively superimposed on all voluntary movements, and patient becomes demented, and after about 12 years dies. The disease is inherited as a Mendelian dominant condition, so half the children of an affected person can expect to become affected. The condition is unusual in its late age at onset so that an individual who is destined to have the disease has often completed his family before he becomes affected. It is not a common condition — there are about 200 cases in south-east of Scotland — but, because of its nature all those at risk, and their spouses as well as the patients themselves, are in a very serious way involved.

We have been interested in the subject for a number of years. We have written two papers, and a former member of the Department has completed a Ph.D. thesis on it and has recently graduated. We have a continuing interest in these families and help them with advice and support. We have recently formed a Huntington's Chorea Association for Scotland so that we can keep in touch with them. We also are closely associated with a similar research which is conducted in the west of Scotland, where many of the affected families are related to ours. We were, in any case, about to seek financial support to continue our research. We are particularly interested in the well-being of those already suffering from the condition, but of course preventive aspects also concern us. There are also a number of extremely interesting genetical problems associated with the disease — the search for linkage with the gene associated with Huntington's chorea, the search for environmental and other genetic factors which are responsible

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for the very great variability in manifestation and even greater variability in age on outset. (Our youngest affected case started at the age of eight years, the oldest at over 70.)

We request, therefore, that the Ludovici Bequest should be allocated to this Department to continue the studies of Huntington's chorea.

The meaning of the testator is that the bequest should be made to study the result of racial crossing (which does not mean only Negro × Caucasoid) without limitation of aspect, and the reply is to limit it for the study of Huntington's chorea, of which, according to the professor of the Department, it has only a limited number of cases in any event, and which would successfully divert the funds from the wider field of racial crossing.

We are told that this is a delicate study to investigate, and surely that is where the rub comes. The University will take the money but it is unwilling to spend the funds on the purpose for which the testator is prepared to give the bequest. All else is really irrelevant.

When we consider Professor Gedda's work on racial crossing, supported by the researches of Doctors A. Serio and A. Mercuri (*Meticciato di Gerra e altri Casi*) or, at the other extreme, *The Blending of Races*, edited by Noel P. Gist and Anthony Gary Dworkin, there is quite evidently room for research in this field. Or if we go to a much earlier study, the Smithsonian publications on the Jukes Case, we have other instances of mixed race, and from this the conclusions which have been drawn for or against a particular form of racial crossing.

If we are to have universities refusing to carry out research because they fear that there will be a certain amount of popular criticism against them for doing so, then we have a degree of suppression of the facts of the case. Ludovici did not demand that they were to find that the white races should prove superior to the black races: or that the crosses would prove to be bad between the two stocks. He merely asked that scientific research should be done.

We have, therefore, the case that the University assumes at once that the white races should be influenced deleteriously by the crossing with Negroids, and it is not prepared to carry out such researches. This means, in fact, that the University is suppressing facts, and is prepared to go on a course of research which assumes that nothing at all happens when the races of man are crossed.

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The Evolution of the Specifically Human Regions of the Hominid Cerebral Cortex*

By V. I. KOTCHETKOVA

The cerebral cortex in the case of man is actually comprised of sectors, which are distinguished from the point of view of their architectonics by an extremely complex organization, while from the point of view of their function they realize strictly human forms.

Russian anthropologists attribute a great importance to the establishment of the factors of the formation of specifically human traits in general and of the cerebral characteristics in particular. The Anthropological Institute of the University of Moscow has organized a laboratory for the study of the evolution of the brain, whose work is directed by the medical doctor J. G. Chevtchenko. The work of this laboratory is principally dedicated to the study of the transformation of the brain in the course of the evolution of the primate order. Very particular attention is attached to the period of the formation of man. The results obtained by the laboratory staff are presented in this paper.

We have established that the cytoarchitectonic areas 39 and 40, however characteristic of man, exist also in the case of the monkey. The structure of these areas is clearly distinguished from that of the adjacent areas and presents a qualitatively new formation, possessing a more complex structure. The surface of the areas in the case of the monkey varies from one species to the other.

The increase of the surface of the areas is not solely due to the progressive evolution of the primates in general, but principally to the degree of development of the manipulative function. For the Platyrrhine monkeys the areas of the inferior parietal region are more developed in the case of *Cebus capucinus*, which is at the same time the Platyrrhine monkey that possesses the most varied and the most complicated manipulative processes. The degree of development of these areas in the case of *Cebus capucinus* surpasses that of numerous Catarrhines including the gibbon. In the case of the latter the surface of areas 39 and 40 is weak. This is probably due to an over great specialization of the anterior members of the gibbon — of giving preference to them as an organ of locomotion. This, of course, considerably

* V. I. Kotchetkova, " L'évolution des régions spécifiquement humaines de l'écorce cérébrale chez les Hominidés." *Proceedings, Sixth International Congress of Anthropological and Ethnological Sciences, Paris,* 1960, Vol. 1. pp. 623-630. Translated by Donald A. Swan.

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diminishes the possibility of employing the anterior members in order to become acquainted with objects and to manipulate them. This is not so in the case of the chimpanzee. This primate is only partially a brachiator. With respect to movement of the superior extremities and the handling of tools, these properties are more developed in the case of the chimpanzee than in the case of the other primates. Areas 39 and 40 of the brain are incomparably larger in the case of the chimpanzee. They occupy nearly the entire inferior parietal region, which calls to mind the characteristic disposition of the actual human brain.

The cytoarchitectonic areas 39 and 40, however specific to man, have homologues in the form of areas appearing in the primates at the same time as the movement of the extremities and the manipulation of tools.

Analysis of the cellular and fibrous structure of areas 4, 5 and 6 in the primates has shown that the surface of the areas and the complexity of their structure is directly proportional to the degree of development of the manipulative function. As for the correlation that exists between the visual sensations and the structure of the cerebral cortex of the occipital region, we have established that the areas of the visual region (17, 18, 19) are larger and possess a more complicated cellular and fibrous structure in the case of the arboreal forms. That is to say, the reaction of orientation and of analysis is more varied than in the case of the terrestrial forms.

It has also been established that in the course of the Quaternary the growth of the brain was not uniform. It follows that the surface of the endocranial casts of fossil men has, as a general rule, a clearly pronounced relief. The sectors of the endocranial cast corresponding topographically to the specifically human regions of the brain show the most pronounced relief and the greatest variation of these parts. Furthermore, we observe a certain parallelism in the process of the transformation of the brain of fossil man with the development of culture. The growth of the cerebral cortex deviates irregularly above all with the appearance of culture.

Already in the case of the Australopithecines (i.e., in the case of *Australopithecus africanus*) the macrostructure of the brain comes near that of the present-day monkey. The endocranial cast of *Australopithecus* is rounded, it has a regular vault, and it does not possess any considerable prominences.

From the time that ancient man engaged in the most elementary forms of work, we begin to observe a certain discord in the variation of the brain. This consists of a more rapid growth of certain of the sectors of the brain in comparison with others, giving occasion to the appearance of prominences.

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It is thus that in the case of Sinanthropus, who constructed the most primitive tools of Chellean-Acheulean type, we observe several prominences on the surface of the endocranial cast. The most accentuated prominence is situated around the extremity of the Sylvian fissure. The second (in order of size) is situated in the posterior part of the inferior frontal convolution. The third prominence is found in the region of the impression of the coronary suture. The comparison of the endocranial cast of Sinanthropus with that of present-day man shows that the focus of intense development of the cerebral cortex is, in the case of Sinanthropus, at the same places as the specifically human regions. At the same time the greatest focus of development in the case of present-day man corresponds to the place where are disposed the cortical zones of the complex functions which the hand accomplishes during the processes of work and of writing. It concerns the zones of praxis, of the evaluation of the spatial proportions of one's own body, of environmental objects, and also the zone of writing. The second focus of development is situated in the language motor zone, while the third focus is that of the somato-topical movements. Such a development is probably not fortuitous. It is not independent of the aggregate of functions which emerge in primitive society with work, with the necessity of analyzing the properties of stone and of wood out of which are formed the first tools. It is not independent of the necessity of a co-ordination and of a complex series of acts during the manufacture of them. It can be the same of a new mode of contact — of the first elements of articulate language.

Later on the modification of the specifically human regions of the brain was quite complex.

In the case of the Neanderthals, these sectors, each remaining the focus of an intense growth, are further divided with respect to manifestations of the variation. The inferior parietal focus is divided into two epicenters: the anterior epicenter and the posterior epicenter. It is now the posterior part which has become the most intense focus of development. The transverse concurrence on a level with this sector shows that the parietal formations very much overhang the temporal formations. In the frontal lobe a second focus is developed more in the lateral direction than in the frontal direction, while a third focus is displaced on the side of the occiput as a consequence of the growth of the anterior frontal formation.

The epoch during which the Neanderthals lived occupies in its aggregate a rather long period of anthropogenesis. It can be characterized as the period of the assimilation by man of the operations of work. It is a period of relatively weak utilization of the technique of treatment of stone and of a long period of

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investigating new procedures of work and new materials.

In the course of this period the hand is perfected. The strokes became more precise and more proportional, more nimble. The forces had to be checked. This was the epoch where the process of establishing the purpose of each of the tools was developed and where for the first time were differences according to the procedures of work.

During the accomplishment by present-day man of the activities which we have just enumerated, the greatest functional pressure is assumed in the sectors of the cerebral cortex where are disposed the cortical extremities connected first with the processes of denervation, second with the manual motor movements, third with the knowledge of the properties of objects and of spatial proportions during the stereotyped acts of work, and finally with the sequence of these in the course of time. That is to say, we are concerned with the cytoarchitectonic areas of the anterior parts of the frontal region and the area 39 disposed to the posterior part of the inferior parietal lobe.

The abrupt changes, which are observed on the endocranial casts of the Neanderthals in the regions in question identical with those which have been described on the brain of present-day man, can serve as evidence of the fact that work assumes the rôle of creator of new forms in the course of anthropogenesis. At the same time, the growth of the inferior frontal parts of the endocranial cast gives indirect evidence of the process of a subsequent development of language.

As a consequence of the irregular development of the brain in the course of anthropogenesis, the qualitative relations of the cytoarchitectonic areas in the case of the present-day man differ significantly from those of the present-day primates. In the case of modern man the relative expansion of certain areas is greater, that of others smaller, that of others yet analagous.

The work of our laboratory and of the Brain Institute has permitted the drawing of a schematic map illustrating the modifications happening in the course of evolution, with the distribution of the surface of the areas of the cerebral cortex. It happens that in the course of the process of evolution the areas of the parietal region (39 and 40) and certain areas of the frontal region (46, 10, 44, 45, 6) and temporal region (37, 38, 41, 42) are enlarged. At the same time the areas of the superior parietal region (7), of the post central convolution (1, 2, 3, 5) and of the median surface of the brain have a relatively constant extension in the case of the primates as in the case of man. The other areas of the cerebral cortex in the case of man are, in so far as their relative dimensions are concerned, inferior to those of the primates.

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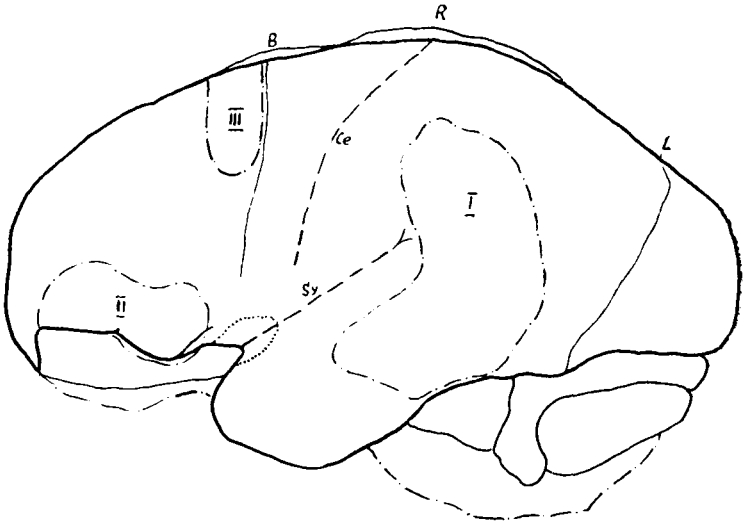
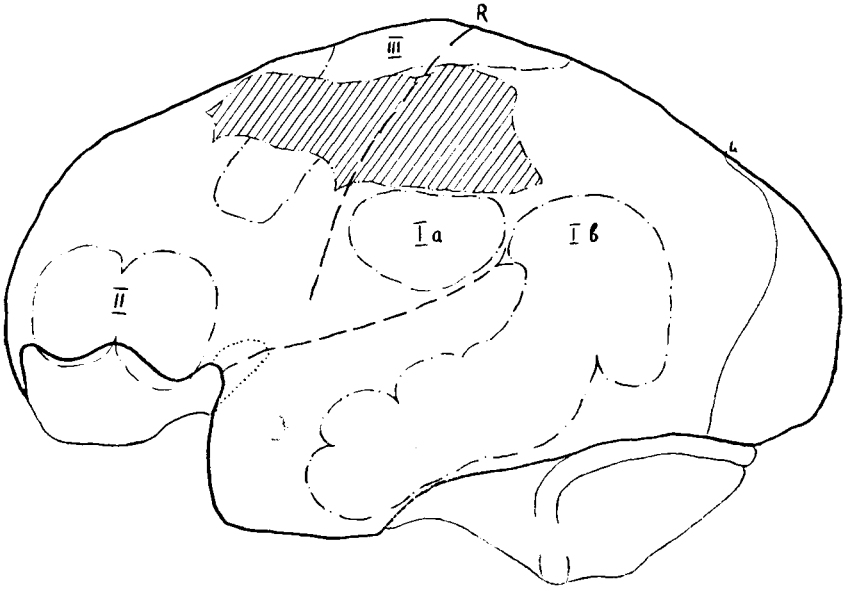
FIGURE 1



The endocranial cast of Sinanthropus
I. The inferior parietal focus; II. The inferior frontal focus; III. The prefrontal focus.

FIGURE 2



The endocranial cast of the Chappelle-aux-Saints fossil
Ia. The anterior epicenter of the parietal focus; Ib. The posterior epicenter of the parietal focus.

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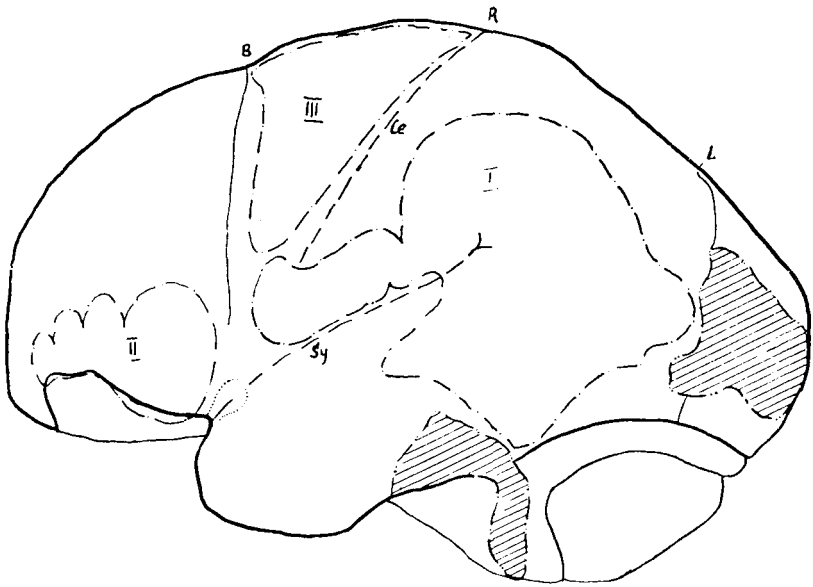
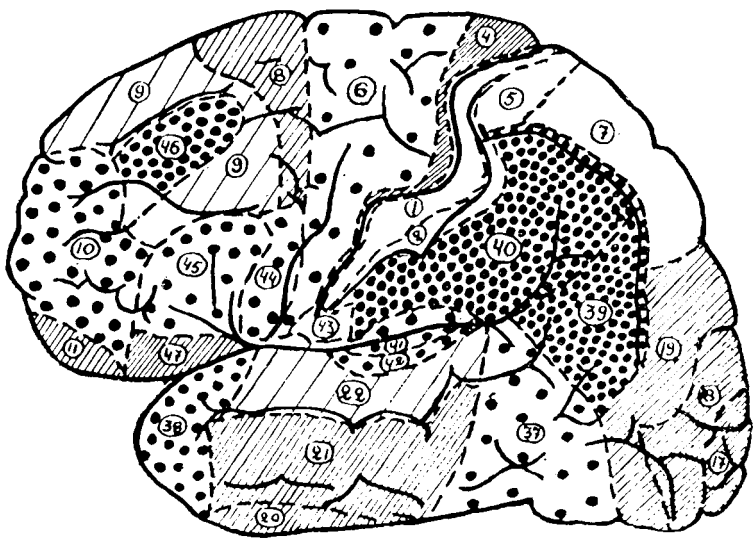
FIGURE 3



The endocranial cast of the Techik-Tach fossil

FIGURE 4



Schematic map of the unequal evolution of the cerebral cortex
Dotted regions: The cortical areas which have increased. Shaded regions: The cortical areas which have decreased.

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The comparison of these data with the functional maps of the brain shows that these are the areas which are connected in the case of man with active oral and written language (the areas of the inferior frontal, inferior parietal, and temporal regions), as well as the areas connected with the movements of the superior extremity and the praxis (the areas of the frontal region and of the parieto-temporal complex) which have become larger.

Given a parallel distribution of the focus of intense growth on the endocranial cast and the coincidence of the aggregate of the reproduced data, there is little probability that the phenomena mentioned are accidental. The comparative macro- and microscopic methods give evidence in this case of a tendency of the totality of development of the brain. This, in spite of its labile character and interchangeability of functions, is formed in response to concrete conditions.

In the case of the primates these are the elements which are connected with the development of the manipulative function, the handling of instruments, and the forms of communication which constitute the new formations of morphofunctional order.

The more complex processes, thanks to which man has ceased to belong to the animal kingdom, have evolved from this base. The principal condition was the initiation of work and of certain forms of communication which were due to it — indeed. the spoken and written language.

IMPORTANT REPRINT

Practical Considerations which are Fundamental in Bantu Affairs in Rhodesia and for an Understanding of Negroid-Caucasoid Problems Generally

by R. GAYRE OF GAYRE

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The Anthropology of the Brain

1. The Structure and the Functioning of the Brain

By DONALD A. SWAN

INTRODUCTION

Human behavior "is related to neurological structure and function just as is its counterpart in lower forms."[1] The physiological basis of learning and intellectual activity in man is the brain—or rather, the central nervous system.[2] And as Williams (1960) concludes, "the functioning of human minds is without doubt closely correlated with brain anatomy and function."[3]

During the past century much has been learned of the anatomy and physiology of the human brain.[4] Animal experiments and psychosurgery research have added to our knowledge of brain functioning. Investigations of electrical and chemical activity in the brain have provided new insights into the physical basis of learning and intelligence, as well as behavioral disorders.[5] Consequently, some progress has been made towards relating differences in brain structure and functioning to individual psychological differences.

The human brain is also the product of evolution, just as is human morphology and behavior. Detailed investigations of fossil remains and comparative analyses of human and other living primates have provided much information on the evolution of the brain.[6] The selective forces governing human evolution and raciation, however, have operated in different directions and at different rates of speed on the different continents. Thus, differential selective pressures accumulated over long periods of time have brought about frequency differences in the distribution of both physical and behavioral traits in human populations.

[1] Ernest Gardner, *Fundamentals of Neurology*, W. B. Saunders, Philadelphia, 1963, p. 261.

[2] Carleton S. Coon *The Origin of Races* Alfred A. Knopf, New York, 1962, p. 337: ". . . The seat of intelligence is the central nervous system. The regulation of self-control is the combined task of the brain and endocrine system, and indeed the brain and endocrines act together in many ways, and influence each other by a complex feedback system."

[3] Roger J. Williams, "Why Human Genetics?" *Journal of Heredity*. Vol. 51, No. 2, 1960, p. 95.

[4] Gerhardt von Bonin, *Essay on the Cerebral Cortex*, Thomas, Springfield, Illinois, 1950, pp. 5-16.

[5] Clifford T. Morgan, *Physiological Psychology*, McGraw-Hill, New York, 1965, pp. 530-567.

[6] Ralph L. Holloway, "The Evolution of the Primate Brain: Some Aspects of Quantitative Relations," *Brain Research*, Vol. 7, 1968, pp. 121-172; W. E. Le Gros Clark, *The Antecedents of Man* (third edition), University of Edinburgh Press, Edinburgh, 1971.

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With this foundation it has been possible to begin the study of the anthropology of the brain. For during the past few decades a number of studies have been conducted on racial and population differences in the size, shape, structure and functioning of the brain. It is the purpose of this series of articles to summarize and review these studies. The series will comprise eight articles on the Anthropology of the Brain: 1. The Structure and Functioning of the Brain; 2. The Evolution of the Brain; 3. Race, Cranial Capacity, and Brain Weight; 4. Race and Brain Structure; 5. Race and Cortical Histology; 6. Race and Electro-Physiology; 7. Race and Brain Chemistry; and 8. Race, Brain and Culture.

THE STRUCTURE OF THE BRAIN

Neurologists have subdivided the central nervous system in a variety of ways in order to delineate its structure and investigate its functioning. The central nervous system comprises the brain and spinal cord. The brain consists of the hindbrain and midbrain, which together form the brain stem, and the forebrain.[7] The principal parts of the brain stem are the medulla, pons, cerebellum and tectum. The cerebellum "is concerned with the co-ordination of muscular movement."[8] Within the brain stem and extending into the hypothalamus of the forebrain is the reticular formation, which is a structure "intimately related to sleep, arousal and attention."[9]

The forebrain is the most important part of the brain for students of physiological psychology, since "it possesses virtually all of the parts concerned in sensation and perception and in the co-ordination of behavior patterns, including those of emotion, motivation, learning, language and thinking."[10] The diencephalon and telencephalon form the two major parts of the forebrain. The diencephalon comprises the optic tracts, pituitary body, thalamus and hypothalamus.[11] The thalamus consists of many nuclei connected with each other, with lower centers of the brain, and with the cerebral hemispheres, and "is the great relay station of the brain."[12] The hypothalamus is the primary neural center for the regulation

[7] Ernest Gardner, *op. cit.*, pp. 8-26.

[8] Donald O. Hebb, *A Textbook of Psychology*, W. B. Saunders, Philadelphia, 1958, p. 67.

[9] Clifford T. Morgan, *op. cit.*, p. 41; H. W. Magoun, *The Waking Brain*, Thomas, Springfield, Illinois, 1963, pp. 53-73.

[10] Clifford T. Morgan, *op. cit.*, p. 41; Ernest Gardner, *op. cit.*, p. 261: "Human behavior is related to neurological structure and function just as is its counterpart in lower forms. Its infinite complexity is correlated with increasing development of the forebrain, particularly the cerebral cortex. Here reside the mechanisms governing language formation and use, emotional reactions and intelligence."

[11] Ernest Gardner, *op. cit.*, pp. 13-18.

[12] Clifford T. Morgan, *op. cit.*, p. 43.

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of endocrine secretions, metabolic activity, body temperature and is "also a center for emotional behavior."[13] In recent years the hypothalamus, together with parts of the cerebral cortex, and certain subcortical structures, has been found to form part of a system, termed the limbic system, which "is important in emotion and related activities."[14]

The principal part of the telencephalon is the cerebral hemispheres, which consist of the corpus striatum, the corpus callosum and the cerebral cortex.[15] The cerebral cortex is a layer of grey matter, composed of nerve cells spread over the convoluted surfaces of the cerebral hemispheres, and in man it is the apparatus of higher mental functions.[16] Each cerebral hemisphere is divided into four lobes—frontal, occipital, parietal and temporal (see Figure 1). The lobes of the cerebral cortex are "characterized by distinctive patterns of internal cortical structure and of subcortical connections."[17]

The cortex of the brain has three primary regions, with well-defined anatomical and physiological boundaries, and distinctive histological texture: (1) the piriform area, or palaeocortex; (2) the hippocampal area, or archicortex; and (3) the neocortex.[18] The first two regions are the phylogenetically older cortex and are concerned with olfactory and visceral processes.[19] The neocortex increases in phylogenesis, so that in mammals it constitutes "the larger and more significant portion of the cerebrum."[20] This progressive development of the neocortex in mammals is correlated "with the increasing importance of auditory, tactile and visual mechanisms."[21]

The many structurally different areas of the cerebral cortex are of two broad classes—the sensory-motor projection areas and the areas of association or elaboration. According to Herrick (1956), "the former areas were differentiated earlier phylogenetically and are each connected by projection fibers with some subcortical part of the brain stem which has a specific analytic function, either

[13] Clifford T. Morgan, *op. cit.*, pp. 46-47.

[14] Clifford T. Morgan, *op. cit.*, p. 52; James W. Papez, "A Proposed Mechanism of Emotion," and Paul D. MacLean, "Psychosomatic Disease and the 'Visceral Brain': Recent Developments Bearing on the Papez Theory of Emotion," in *Basic Readings in Neuropsychology* (edited by Robert L. Isaacson), Harper and Row, New York, 1964, pp. 87-109 and pp. 181-211.

[15] Ernest Gardner, *op. cit.*

[16] C. Judson Herrick, *The Evolution of Human Nature*, University of Texas Press, Austin, Texas, 1956, pp. 368-370.

[17] C. Judson Herrick, *op. cit.*, p. 389.

[18] Gerhardt von Bonin, *op. cit.*, pp. 20-31.

[19] Ernest Gardner, *op. cit.*, p. 265.

[20] Clifford T. Morgan, *op. cit.*, p. 58.

[21] Ernest Gardner, *op. cit.*, p. 266.

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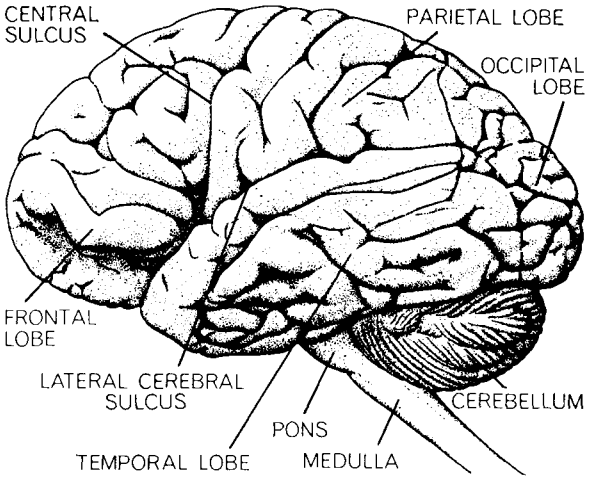
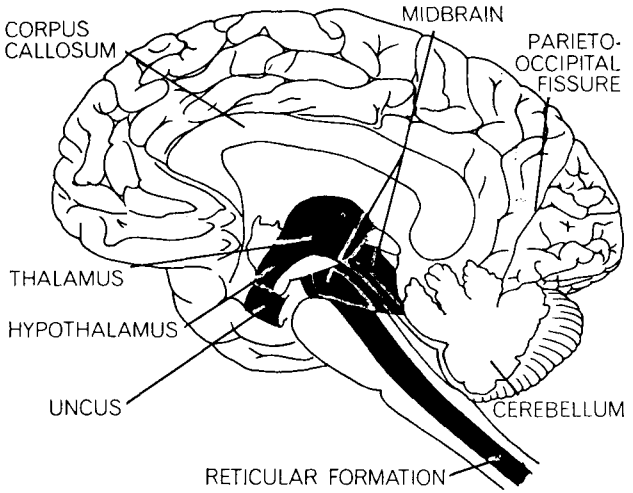
FIGURE 1



The anatomical structure of the human brain (Luria, 1970).

FIGURE 2



The functional organization of the brain: Block 1. This system or block includes the brain stem and the palaecortex and regulates wakefulness and the response to stimuli (Luria, 1970).

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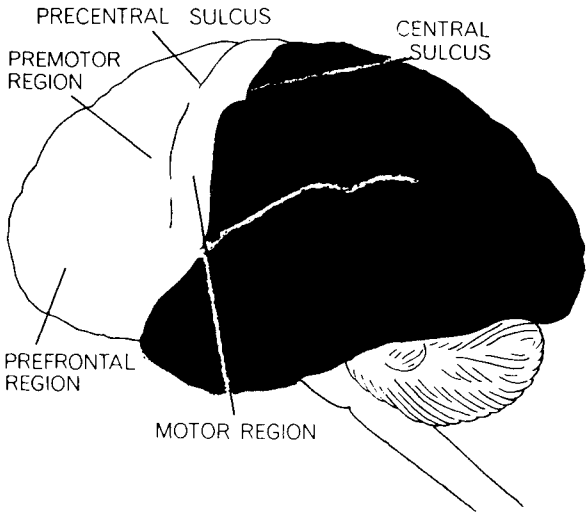
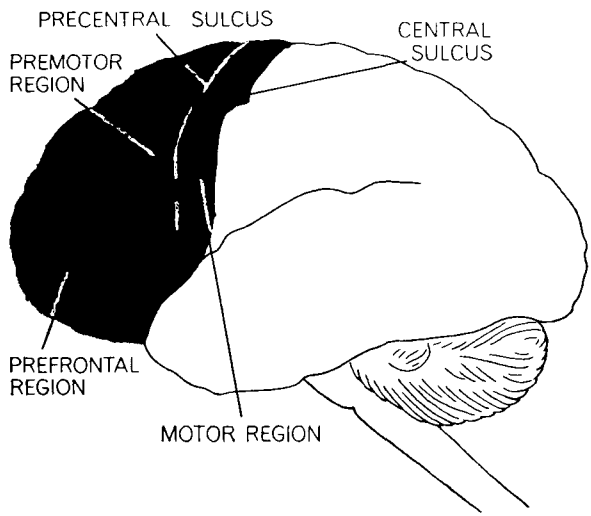
FIGURE 3



The functional organization of the brain: Block 2. This system or block is located in the rear areas of the cortex and plays a decisive rôle in the analysis, coding and storage of information (Luria, 1970).

FIGURE 4



The functional organization of the brain: Block 3. This system or block comprises the frontal lobes and is involved in the formation of intentions and programs for behavior (Luria, 1970).

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sensory or motor.'[22] The association areas serve to bind all parts of the cortex together by association fibers and are "the most important parts of the nervous system as regards mental and emotional processes."[23] Herrick similarly concludes that ". . . the higher psychoneural functions which emerge in consciousness as perception, reasoning and intelligently directed purposive conduct require the participation of more or less of the homotypical cortex of the so-called associational areas."[24] In the human brain "there are two great islands of association cortex: the prefrontal area, anterior to the motor area in the frontal lobe, and a posterior area comprising part of the parietal, occipital and temporal lobes."[25]

Further subdivisions of the cortex have been made by a number of workers according to distinctive patterns of arrangement of the nerve cells and fibers. Brodmann (1904) published a series of maps of cortical areas "based on the cellular structure of the cortex."[26] However, contemporary workers find that most of these small cortical areas "have no constant structural features or functional significance." Herrick, for example, contends that only "a few of Brodmann's areas have well-established functional significance, notably four of the projection centers" and that the "localization of other cortical functions presents difficulty."[27]

In recent years electrical methods have been used to map cortical projection areas. Stimulation of a sense organ has been found to result in an evoked electrical response in corresponding points in the cortical areas to which the sense projects.[28] From the study of patients with epilepsies and focal lesions of the brain, Penfield (1947; 1954) reported that he could map motor responses, somesthetic, acoustic and visual sensations and "hallucinations and perceptual illusions."[29]

Histological studies of the cerebral cortex have also demonstrated that the cells are arranged in more or less well-defined strata or

[22] C. Judson Herrick, *op. cit.*, p. 375.

[23] Ernest Gardner, *op. cit.*, p. 294: "Worthy of special note is the development of neocortex not concerned in sensory or motor functions. . . . Such areas are loosely called 'association' areas because they are related to learned behavior and complex processes. In the frontal lobe, this trend takes the form of increasingly larger prefrontal areas. In the posterior parts of the cerebral cortex, it is seen in increasingly larger parietal and temporal areas outside the known sensory areas."

[24] C. Judson Herrick, *op. cit.*, p. 414.

[25] Donald O. Hebb, *op. cit.*, pp. 83-84.

[26] K. Brodman, *Vergleichende Lokalisations-Lehre der Grosshirnrinde*, J. A. Barth, Leipzig, Germany, 1904.

[27] C. Judson Herrick, *op. cit.*, pp. 389-390.

[28] Clifford T. Morgan, *op. cit.*, p. 51.

[29] Wilder Penfield, "Some Observations on the Cerebral Cortex of Man," *Proceedings on the Royal Society of London* (Series B), Vol. 1343, 1947, pp. 329-347; Wilder Penfield and Herbert Jasper, *Epilepsy and the Functional Anatomy of the Human Brain*, Little, Brown and Company, Boston, 1956, pp. 41-238.

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layers and in most parts of the cortex six layers are usually recognized. These layers "differ in cell density as well as in the type and size of cells which they contain."[30] Ariens-Kappers (1928) concluded that the different cortical layers have "different functions," and that the supra-granular layers are phylogenetically more recent and "the last to differentiate ontogenetically." He also contended that "in extreme idiocy" the supragranular layers "may be more arrested than the granular and subgranular layers."[31]

THE FUNCTIONING OF THE BRAIN

The brain is a mechanism "for the transmission of signals that arise in the peripheral sense organs, are transmitted by the sensory nerves as pulses of electrical potential to the central nervous system and they are variously integrated and then reflected over the motor nerves to result in our behavior."[32] The basic unit or building block of the nervous system is the nerve cell or neuron. Each neuron consists of a cell body, with short branch-like protoplasmic extensions termed dendrites and a long filament or axon which terminates in a brush-like ending.[33]

The human brain contains some ten to 15 billion neurons.[34] "Each of these cells is in functional connection with many others by branching nerve fibers, some of which may reach remote parts of both the same and the opposite cerebral hemispheres. A single cell may receive as many as 100 terminals of these fibers from various sources . . . ."[35] The neurons are in turn supported by "a framework of specialized non-conducting cells known collectively as neuroglia."[36] Shariff (1953) estimates that the nerve cell bodies comprise some five per cent of the total cortical volume,[37] while Hyden (1960) estimates that dendritic processes comprise 25 per cent and glial cells about five per cent of the volume.[38]

[30] Gerhardt von Bonin, *op. cit.*, pp. 43-46.

[31] C. U. Ariens-Kappers, *The Evolution of the Nervous System*, DeErven F. Bohn, Haarlem, Holland, 1928, pp. 144-146.

[32] Percival Bailey, "Cortex and Mind," in *Theories of the Mind* (edited by Jordan Scher), The Free Press of Glencoe, New York, 1962, pp. 3-14.

[33] Ernest Gardner, *op. cit.*, 1962, p. 86.

[34] J. Z. Young, *Doubt and Certainty in Science: A Biologist's Reflections on the Brain*, Oxford, New York, 1960, p. 37.

[35] C. Judson Herrick, *op. cit.*, p. 393.

[36] Ernest Gardner, *op. cit.*, p. 65.

[37] G. A. Shariff, "Cell Counts in the Primate Cerebral Cortex," *Journal of Comparative Neurology*, Vol. 98, 1953, pp. 381-400.

[38] A. Hyden, "The Neuron," in *The Cell* (edited by J. Brachet and A. E. Mirsky). Academic Press, New York, 1960, pp. 215-323; Galambos (1961) has proposed a "glia-neural theory of brain function," based on the view that the glia aid in locking in neuronal pulses, so that the glia-neuron becomes the basic unit of the nervous system. R. Galambos, "A Glia-Neural Theory of Brain Function," *Proceedings of the National Academy of Science*, Vol. 47, 1961, pp. 129-136.

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Nerves transmit impulses that behave much like those of electricity. The neurons "are linked together by synaptic junctions to form conduction pathways for nerve impulses."[39] The impulses enter over the dendrites and pass out along the axon. The nerve-impulse is "a tiny electrochemical storm that sweeps across cell-body and axon; it obeys the all-or-none principle."[40] Hebb (1949) proposed a physiological mechanism to describe the formation of "cell-assemblies" and applied this to "the problems of thinking and of set and attention."[41] Eccles (1953)[42] and Morgan (1965)[43] have reviewed and evaluated the status of research in the field of neuron physiology.

The cerebral cortex "is tied to all parts of the brain stem by elaborate systems of fibers, some of which transmit nervous impulses to the cortex and others from it, so that practically all lower centers are in reciprocal nervous connection with the cortex and are under more or less direct cortical control."[44] Herrick (1956) views the cortex as "a facilitating mechanism" or a "central integrative agency for all bodily functions."[45] The integrative processes which the cortex performs are "circular (feed-back) reactions among the various cortical areas and between the cortex and thalamic and other sub-cortical structures."[46] New insights into the functioning of the brain have been gained by the application of cybernetic concepts,[47] nerve network mechanisms [48] and information theory.[49] The brain is regarded as a sort of computer with the neurons functioning as elements of elaborate circuits. In this view the nervous system "codes sensations, computes orders to be relayed to the muscles and handles all other messages in terms of off-on impulses," with the results being "actions, emotions, ideas."[50]

[39] Ernest Gardner, *op. cit.*, p. 86.

[40] Donald O. Hebb, *op. cit.*, p. 107.

[41] Donald O. Hebb, *The Organization of Behavior: A Neuropsychological Theory*, Wiley, New York, 1949.

[42] John C. Eccles, *The Neurophysiological Basis of Mind*, Oxford, New York, 1953.

[43] Clifford T. Morgan, *op. cit.*, pp. 61-81.

[44] C. Judson Herrick, *op. cit.*, p. 396.

[45] C. Judson Herrick, *op. cit.*, p. 396.

[46] C. Judson Herrick, *op. cit.*, p. 416.

[47] Norbert Wiener, *Cybernetics*, M.I.T. Press, Cambridge, Massachusetts, 1961, pp. 116-132 and pp. 169-204.

[48] Warren S. McCulloch and W. Pitts "A Logical Calculus of the Ideas Immanent in Nervous Activity," *Bulletin of Mathematical Biophysics*, Vol. 5, 1943, pp. 115-133.

[49] W. S. Fields and W. Abbott (editors), *Information Storage and Neural Control*, Thomas Springfield, Illinois, 1963.

[50] John Pfeiffer, *The Human Brain*, Pyramid, New York, 1962, p. 235.

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For a long time there has been a controversy among neurologists as to whether the functioning of the human brain should be viewed in terms of regional localization and specializations (the molecular theory) or in terms of mass action and equipotentiality of function (the molar theory). Psychosurgery research and other experimental work have demonstrated that both principles are operative in the functioning of the human brain. Herrick (1956), for example, differentiates between the analytic processes of the projection centers and the synthetic or integrative processes of the associational tissue. "The former are localized in mosaic patterns, the latter in dynamic patterns involving fluctuating discharge of extensive and in some cases variable areas of cortical and subcortical nervous circuits."[51] Thus, clear-cut localizations in the cortex have been demonstrated for the special sensory and motor areas and the speech area.[52] The various mental processes, however, "are not inflexibly bound to the tissue of any particular area", although there are "some ill-defined regions which are concerned usually and by preference with different types of mental functions."[53]

Learning and memory involve circuits passing through the cortex. That is, records of past experience are believed to be preserved "in the form of some as yet unknown enduring change in the setup of the patterns of cortical activity," termed "engrams," "neurograms," or "memory traces."[54] Learning also involves changes in the physiochemical conditions of the brain cells which make retention

[51] C. Judson Herrick, *op. cit.*, p. 430; also pp. 409-410: ". . . The analytic functions in general are performed by fixed and stable systems of tissues in spatial patterns that are hereditary and similar (with minor variations) in all members of each animal species. The integrative functions, on the contrary, are more labile. They are defined in terms of dynamic patterns of action that persist as patterns of function but are not flexibly bound to any fixed structural pattern. These processes are localized in space *while they are in operation*, but they may operate without significant change of pattern, using any suitable tissue structures that may be available."

[52] Donald O. Hebb, *A Textbook of Psychology*, *op. cit.*, p. 86; Ralph L. Holloway, "The Evolution of the Primate Brain: Some Aspects of Quantitative Relations," *Brain Research*, Vol. 7, 1968, pp. 121-172: "Current opinion views man's cerebral cortex as predominantly homogeneous in structure, rather than greatly differentiated regionally (Bonin and Bailey). This does not assume, however, that all cortical tissue has the same function, as Lashley had earlier thought to be the case. (Here it should be understood that the pre- and post-central gyri, the striate cortex and that of the superior temporal gyrus concerned with audition are not included . . .)."

[53] C. Judson Herrick, *op. cit.*, pp. 416 and 430.

[54] C. Judson Herrick, *op. cit.*, p. 405; Ernest Gardner, *op. cit.*, p. 296: ". . . Learning includes, in the form of memory, relationships between neural processes which may last over scores of years. . . . It has been postulated that closed circuits of nerve cells . . . are involved in memory, because of the possibility of continuous electrical activity . . . . It is much more likely that long-term processes in the nervous system will be found to depend upon chemical reactions and molecular arrangement in nerve cells. . . ."

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and memory possible. Neurologists and psychologists have advanced a variety of theories to interpret the available data on learning and memory. Ariens-Kappers (1921) developed a "neurobiotactic theory of learning," which contended that "the connecting parts of a neuron grow closer together under the influence of the stimuli involved in learning."[55] Hebb (1949) proposed a consolidation theory of memory."[56] Milner (1961) advanced a "sensitization theory," which emphasized the role of transmitter substances, such as acetylcholine, in learning.[57] Hyden (1962) proposed a theory that learning causes certain changes in the lattice structure of the protein molecules of ribonucleic acid (RNA).[58]

Morgan (1965) has reviewed and analyzed much of the recent research on the physiological aspects of learning and memory.[59] Reviews and discussions of current thinking on the neurophysiological basis of mental and behavioral processes, or the "mind-brain problem," have been provided by Bailey (1962),[60] von Bonin (1962),[61] Diamond and Chow (1962),[62] Galambos and Morgan (1960),[63] Hess (1964),[64] Luria (1970),[65] Pribram (1962),[66] Sperry (1964),[67] and Young (1964).[68]

[55] C. U. Ariens-Kappers, "On the Structural Laws in the Nervous System: The Principles of Neuro-Biotoxis," *Brain*, Vol. 44, 1921, p. 125.

[56] Donald O. Hebb, *The Organization of Behavior: A Neuropsychological Theory*, *op. cit.*, 1949.

[57] Peter M. Milner, "The Application of Physiology to Learning Theory," in *Current Trends in Psychological Theory* (edited by Robert A. Patton), University of Pittsburgh Press, Pittsburgh, 1961, pp. 111-133.

[58] H. Hyden, "Satellite Cells in the Nervous System," *Scientific American*, Vol. 205, No. 12, 1961, pp. 62-83.

[59] Clifford T. Morgan, *op. cit.*, pp. 546-567.

[60] Percival Bailey, *op. cit.*, pp. 3-14.

[61] Gerhardt von Bonin, "Brain and Mind," in *Psychology: A Study of a Science. Volume* 4. *Biologically Oriented Fields* (edited by Sigmund Koch) McGraw-Hill, New York, 1962, pp. 100-118.

[62] I. T. Diamond and K. L. Chow, "Biological Psychology," in *Psychology: A Study of a Science. Volume* 4, *op. cit.*, pp. 158-241.

[63] R. Galambos and C. T. Morgan, "The Neural Basis of Learning," in *Handbook of Physiology. Volume* 3 (edited by J Field, H. W. Magoun and V. E. Hall), American Physiological Society, Washington D.C., 1960.

[64] W. R. Hess, *The Biology of the Mind*, University of Chicago Press, Chicago, Illinois, 1964.

[65] A. R. Luria, "The Functional Organization of the Brain," *Scientific American*, Vol. 222, No. 3, 1970, pp. 66-79.

[66] Karl H. Pribram, "Interrelations of Psychology and the Neurological Disciplines," in *Psychology: A Study of a Science. Volume* 4, *op. cit.*, pp. 119-157.

[67] R. W. Sperry, "Neurology and the Mind-Brain Problem," in *Basic Readings in Neuropsychology*, *op. cit.*, pp. 403-429.

[68] J. Z. Young, *A Model of the Brain*, Oxford, New York, 1964.

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Luria (1970), for example, has proposed a detailed model of the functional organization of the brain on the basis of his studies of brain injuries. In his view the human brain is comprised of three major functional systems or blocks. The first block includes the brain stem and palaeocortex and "regulates wakefulness and the response to stimuli" (see Figure 2). The second block is located in the rear areas of the cortex and is regarded as playing "a decisive rôle in the analysis, coding and storage of information" (see Figure 3). The third block comprises the frontal lobes and "is involved in the formation of intentions and programs for behavior" (see Figure 4). Observations of injuries to the brain combined with factor analyses of batteries of psychological tests have provided additional information on the location of specific parts of the various functional systems of the brain, such as the system of sensory signals and the spatial field, and of the brain systems involved in complex psychological processes, such as the abilities to speak and write, perception, performance of planned actions, memorization, problem-solving, *et al.*

In the course of investigating the structure and functioning of the human brain, neurologists have found considerable individual and group variability in cerebral structure. Lashley (1947) noted that "individual variation in brain structure within a species is of the same kind and often equal in extent to that between species."[69] Delgado (1965) described the difficulties in implanting electrodes within the brain which require "a detailed and complex exploration in each individual, because of the existence of anatomical and physiological variability."[70] Lashley and Clark (1946) also observed "individual variations in cell size, density and arrangement of the cortex" and concluded that "marked local variations in cell size and density among individuals of the same species may constitute a basis for individual differences in behavior."[71]

The brain, however, functions as a total system. Much current research is based upon the application of cybernetic concepts to the study of brain functioning.[72] Investigators have generally studied one aspect of the structure and functioning of the brain in isolation, due to the complexity of the subject matter. Such studies can, of course, only yield a partial explanation of the neurophysiological basis of individual and group differences in mental ability and behavior. Many studies, however, have been conducted along these lines, which will be reviewed in subsequent articles in this series.

[69] K. S. Lashley, "Structural Variation in the Nervous System in Relation to Behavior," *Psychological Review*, Vol. 54, 1947, pp. 325-334.

[70] Jose M. R. Delgado, *Evolution of the Physical Control of the Brain*, American Museum of Natural History, New York, 1965, p. 50.

[71] K. S. Lashley and G. Clark, "The Cytoarchitecture of the Cerebral Cortex of Ateles," *Journal of Comparative Neurology*, Vol. 25, 1946, pp. 223-305.

[72] F. H. George, *Cybernetics and Biology*. W. H. Freeman and Company, San Francisco, 1965, pp. 113-123.

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SUMMARY

The physiological basis of learning and behavior in man is the central nervous system. The central system comprises the brain and spinal cord. The cerebral hemispheres of the brain consist of the corpus striatum, the corpus callosum and the cerebral cortex. The cerebral cortex is a layer of grey matter composed of nerve cells spread over the convoluted surface of the cerebral hemispheres. In man it is the apparatus of higher mental functions. The cerebral cortex is comprised of two broad classes of structurally different areas—the sensory-motor projection areas and the association areas. Further subdivisions of the cortex into cortical areas on the basis of distinctive nerve cell and fiber patterns have been made by some students of the brain. Histological studies have also demonstrated that the cells of the cerebral cortex are arranged into six more or less well-defined strata or layers with different functions.

The brain is a mechanism for the transmission of signals arising in the peripheral sense organs and transmitted to the central nervous system, where they are integrated and then reflected over the motor nerves to result in behavior. The basic unit or building block of the nervous system is the nerve cell or neuron. The human brain contains some ten to 15 billion neurons. The neurons are linked together by synaptic junctions to form conduction pathways for nerve impulses. The nerve-impulse is a tiny electro-chemical storm that sweeps across the cell-body and axon and obeys the "all-or-none" principle.

The cerebral cortex may be viewed as a "facilitating mechanism" or "central integrative agency" for all bodily functions. Students of the functioning of the brain differentiate between the analytic processes of the projection centers and the synthetic or integrative processes of the associational tissue. The former are localized in mosaic patterns, the latter in dynamic patterns involving fluctuating discharge of extensive and in some cases variable areas of cortical and subcortical nervous circuits. Learning and memory involve circuits passing through the cortex. These are integrated dynamic systems that comprise the same arrangements of nervous elements, termed a "cell-assembly." Learning also involves changes in the physiochemical conditions of the brain cells which make memory and retention possible. Current research into the functioning of the brain is focusing upon the application of cybernetic concepts, nerve network mechanisms and information theory.

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The Anthropology of the Brain

2. The Evolution of the Primate and Australopithecine Brain

By DONALD A. SWAN

INTRODUCTION

Man is as much the product of evolution as other forms of life.[1] However, man differs from all other animals in the possession of behavioral properties such as toolmaking, the use of fire and speech.[2] The development of such specifically human behavioral attributes is no doubt related to evolutionary changes in the brain in man. Students of the evolution of the brain employ two methods of study in their investigation of these changes: palaeoneurology and comparative neurology. "The former studies the changes in structure as they appear in the fossil record, while the latter attempts to understand better the nature of extant forms through study of structure and function."[3]

Apart from comparisons of brain size—or rather, of cranial capacity—palaeoneurology is limited to an examination of the surface features of the brain as determined from endocasts. Holloway (1968), however, contends that "the study of primate endocasts, particularly in the great apes and hominids, gives exceeding little information about evolutionary changes," with the visible markings on the endocasts being "extremely variable in both relief and form."[4] The second method of comparative neurology—which involves comparative study of the extant brains of monkeys, apes and men, for example—also has its limitations. The three forms are "the end result of three lines of evolution." Hence, a comparative study of the brains of these forms does not chronicle the "actual evolutionary changes of the organ in any one group" nor is it "a direct study of the evolution of man."[5]

Despite these limitations students of the brain have employed findings from the fields of palaeoneurology and comparative neurology in an effort to delineate the evolutionary changes in the brain and the processes by which they have occurred. Some of the

[1] Ernst Mayr, *Animal Species and Evolution*, Harvard University Press, Cambridge, 1963, p. 624.

[2] Carleton S. Coon, *The Origin of Races*, Alfred A. Knopf, New York, 1962, p. 73.

[3] Ralph L. Holloway, "The Evolution of the Primate Brain: Some Aspects of Quantitative Relations," *Brain Research*, Vol. 7, 1968, p. 121.

[4] *Ibid.*

[5] *Ibid.*

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earlier workers in these fields—Sir Grafton Elliot Smith (1927),[6] Sir Arthur Keith (1931),[7] C. U. Ariens-Kappers (1929)[8]—relied primarily on information obtained from the endocranial casts of living primates and fossil men. Later workers—Connolly (1950),[9] von Bonin (1963),[10] Le Gros Clark (1971)[11]—tended to be more cautious in their use of endocranial cast data and to rely more on the findings from the field of comparative neurology. Von Eickstedt (1959),[12] attempted to develop a science of palaeopsychology by interrelating data from the fields of palaeontology, developmental psychology, cultural anthropology and palaeoneurology. Magoun (1960),[13] provided a useful survey of knowledge of "The Evolution of Man's Brain" from the standpoint of a neuro-anatomist. Holloway (1968),[14] recently conducted a detailed critical review of much of the published literature on the evolution of the primate brain.

It is the purpose of this series of articles to review and analyze the writings of these and other students of the brain in an attempt

[6] Sir Grafton Elliot Smith, *Essays on the Evolution of Man*, Oxford University Press, Oxford, 1927.

[7] Sir Arthur Keith, *New Discoveries Relating to the Antiquity of Man*, Williams and Norgate, London, 1931.

[8] U. Ariens Kappers, *The Evolution of the Nervous System in Invertebrates, Vertebrates and Man*, De Erven F. Bohn, Haarlem, Holland, 1929.

[9] Cornelius J. Connolly, *External Morphology of the Primate Brain*, C. C. Thomas, Springfield, Illinois, 1950, p. 270: "The degree in which the form and fissuration of the brain are reproduced in endocranial casts is of much interest. If the details of fissuration are reproduced to a considerable degree, the findings may be of great importance in assigning the relative status of specimens of fossil primate forms. Some investigators have described such details on the endocranial casts of fossil man, while others have been quite skeptical of learning anything with certainty of the fissuration from endocranial casts."

[10] Gerhardt von Bonin, *The Evolution of the Human Brain*, University of Chicago Press, Chicago, 1963, p. 41: "What can legitimately be deduced from endocranial casts about the brain which they purport to portray? Much that we have gathered from the literature is of little value, since it is based on mistaken premises and homologies which can hardly be expected to survive a more critical examination."

[11] W. E. Le Gros Clark, *The Antecedents of Man*, University of Edinburgh Press, Edinburgh, Scotland, 1971, p. 262: "Attempts have been made to delineate the details of the convolutional pattern of *Homo erectus* and other extinct types of hominid from endocranial casts, but the identification of individual sulci and gyri by such means is far too insecure to permit of positive statements or conclusive inferences."

[12] Egon von Eickstedt, "Stammesgeschichte des Seelischen (Paläo-psychologie)," in G. Herberer (editor), *Die Evolution der Organismen*, Gustav Fischer, Stuttgart, Germany, 1959, Vol. II, pp. 1,192-1,237.

[13] H. W. Magoun, L. Darling and J. Prost, "The Evolution of Man's Brain," in M. A. B. Brazier (editor), *The Central Nervous System and Behavior*, Josiah Macy Foundation, New York, 1960, pp. 33-126.

[14] Ralph L. Holloway, *op. cit.*, pp. 1,192-1,237.

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to trace the development of the brain of living man through the various stages of hominid evolution. The first part of the series will briefly survey the development of the brain during the long period of primate evolution and the major stages of hominid evolution—the Australopithecine stage, the Pithecanthropine or *Homo erectus* stage, the Neanderthal stage, and that of modern man or *Homo sapiens*. The second part of the series will deal with the relation between hominid behavioral properties—such as language and manipulative ability—and changes in the size and structure of the brain.

PRIMATE EVOLUTION

The emergence and progressive evolution of the primate order occurred during the Tertiary epoch. Estimates of the duration of past geological periods have been greatly extended in recent years due to the development of new and more accurate methods of dating. These include the uranium-lead method and the potassium-argon method. Thus, Le Gros Clark (1971) now considers the total length of time occupied by the evolution of the primates to be more than 80 million years. His estimates of the duration of the six successive geological periods of the Tertiary epoch are provided in Table 1.[15]

TABLE 1

*Estimated duration of the successive periods of the Tertiary epoch** (Le Gros Clark, 1971)

Geological period	*Duration in years*
Pleistocene	3,000,000
Pliocene	15,000,000
Miocene	20,000,000
Oligocene	10,000,000
Eocene	20,000,000
Palaeocene	15,000,000
Total Tertiary epoch	83,000,000

* The successive periods are listed in their time sequence and stratigraphical level from the most recent—the Pleistocene—to the oldest—the Palaeocene.

The living primates have been classified into a variety of suborders, families and genera on the basis of comparative anatomical and physiological studies and analyses of the fossil record. Simpson's (1945) taxonomy which begins with a division of the primate order into the two suborders of prosimii and anthropoidea, is

[15] W. E. Le Gros Clark, *op. cit.*, p. 36.

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TABLE 2

The taxonomy of the primates
(Simpson, 1945)

Order primates

Suborder Prosimii
Infraorder Lemuriformes
Superfamily Tupaioidea
Lemuroidea
Daubentonioidea
Infraorder Lorisiformes
Infraorder Tarsiiformes
Superfamily Tarsioidea

Suborder Anthropoidea
Superfamily Ceboidea
Cercopithecoidea
Hominoidea

presented in Table 2.[16] The morphological criteria employed in earlier taxonomies have in recent years been supplemented by serological studies and comparative analyses of the molecular structure of hemoglobins and protein molecules. Simons (1964) has consequently proposed an elaborate taxonomy of the living primates which comprises some 52 different genera (see Table 3).[17]

Attempts to construct a phylogeny of the primates tracing the order from its beginnings in the Palaeocene period have been hampered by the fragmentary nature of the fossil record. This is presumably due to the fact that the main lines of the evolutionary development of the Anthropoidea "were followed by arboreal creatures whose natural habitat was in forested regions."[18] Simons (1964) has recently reviewed and summarized the available primate fossil material. His reconstruction of primate phylogeny is presented in Figure 1.[19]

Primate biochemistry has demonstrated a close relationship between man and the large anthropoid apes—in particular the gorilla and the chimpanzee—a less close relationship with the Catarrhine monkeys and no more than a distant relationship with the lower primates.[20] Hence, the Hominidae—the zoological family of which *Homo sapiens* is the only surviving species—and the

[16] G. G. Simpson, "The Principles of Classification and Classification of Mammals," *Bulletin of the American Museum of Natural History*, Vol. 85, 1945, pp. 1-350.

[17] Elwyn L. Simons, "The Early Relatives of Man," *Scientific American*, Reprint No. 622, 1964, pp. 4-5.

[18] W. E. Le Gros Clark, *op. cit.*, p. 339.

[19] Elwyn L. Simons, *op. cit.*, p. 7.

[20] W. E. Le Gros Clark, *op. cit.*, p. 19.

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TABLE 3

The taxonomy of living primates (Simons, 1964)

Order	*Suborder*	*Infraorder*	*Superfamily*	*Family*	*Subfamily*	*Genus*	*Common name*
	Prosimii	Lemuriformes	Tupaioidea	Tupaiidae	Tupaiinae	*Tupaia*	Common tree shrew
						Dendrogale	Smooth-tailed tree shrew
						Urogale	Philippine tree shrew
					Ptilocercinae	*Ptilocercus*	Pen-tailed tree shrew
			Lemuroidea	Lemuridae	Lemurinae	*Lemur*	Common lemur
						Hapalemur	Gentle lemur
						Lepilemur	Sportive lemur
					Cheirogaleinae	*Cheirogaleus*	Mouse lemur
						Microcebus	Dwarf lemur
				Indridae		*Indri*	Indris
						Lichanotus	Avahi
						Propithecus	Sifaka
				Daubentoniidae		*Daubentonia*	Aye-aye
		Lorisiformes	Lorisoidea	Lorisidae		*Loris*	Slender loris
						Nycticebus	Slow loris
						Arctocebus	Angwantibo
						Perodicticus	Potto
				Galagidae		*Galago*	Bush baby
		Tarsiiformes	Tarsioidea	Tarsiidae		*Tarsius*	Tarsier
				Callithricidae		*Callithrix*	Plumed and pygmy marmosets
						Leontocebus	Tamarin
					Callimiconinae	*Callimico*	Goeldi's marmoset

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Primates	Anthropoidea	Platyrrhini	Ceboidea	Cebidae	Aotinae	*Aotes*	Douroucouli
						Callicebus	Titi
					Pithecinae	*Pithecia*	Saki
						Chiropotes	Saki
						Cacajao	Uakari
					Alouattinae	*Alouatta*	Howler
					Cebinae	*Cebus*	Capuchin
						Saimiri	Squirrel monkey
					Atelinae	*Ateles*	Spider monkey
						Brachyteles	Woolly spider monkey
						Lagothrix	Woolly monkey
		Catarrhini	Cercopithecoidea	Cercopithecidae	Cercopithecinae	*Macaca*	Macaque
						Cynopithecus	Black ape
						Cercocebus	Mangabey
						Papio	Baboon drill
						Theropithecus	Gelada
						Cercopithecus	Guenon
						Erythrocebus	Patas monkey
					Colobinae	*Presbytis*	Common langur
						Pygathrix	Douc langur
						Rhinopithecus	Snub-nosed langur
						Simias	Pagi Island langur
						Nasalis	Proboscis monkey
						Colobus	Gueraza
			Hominoidea	Hylobatidae		*Hylobates*	Gibbon
						Symphalangus	Siamang
				Pongidae		*Pongo*	Orang-utan
						Pan	Chimpanzee
						Gorilla	Gorilla
				Hominidea		*Homo*	Man

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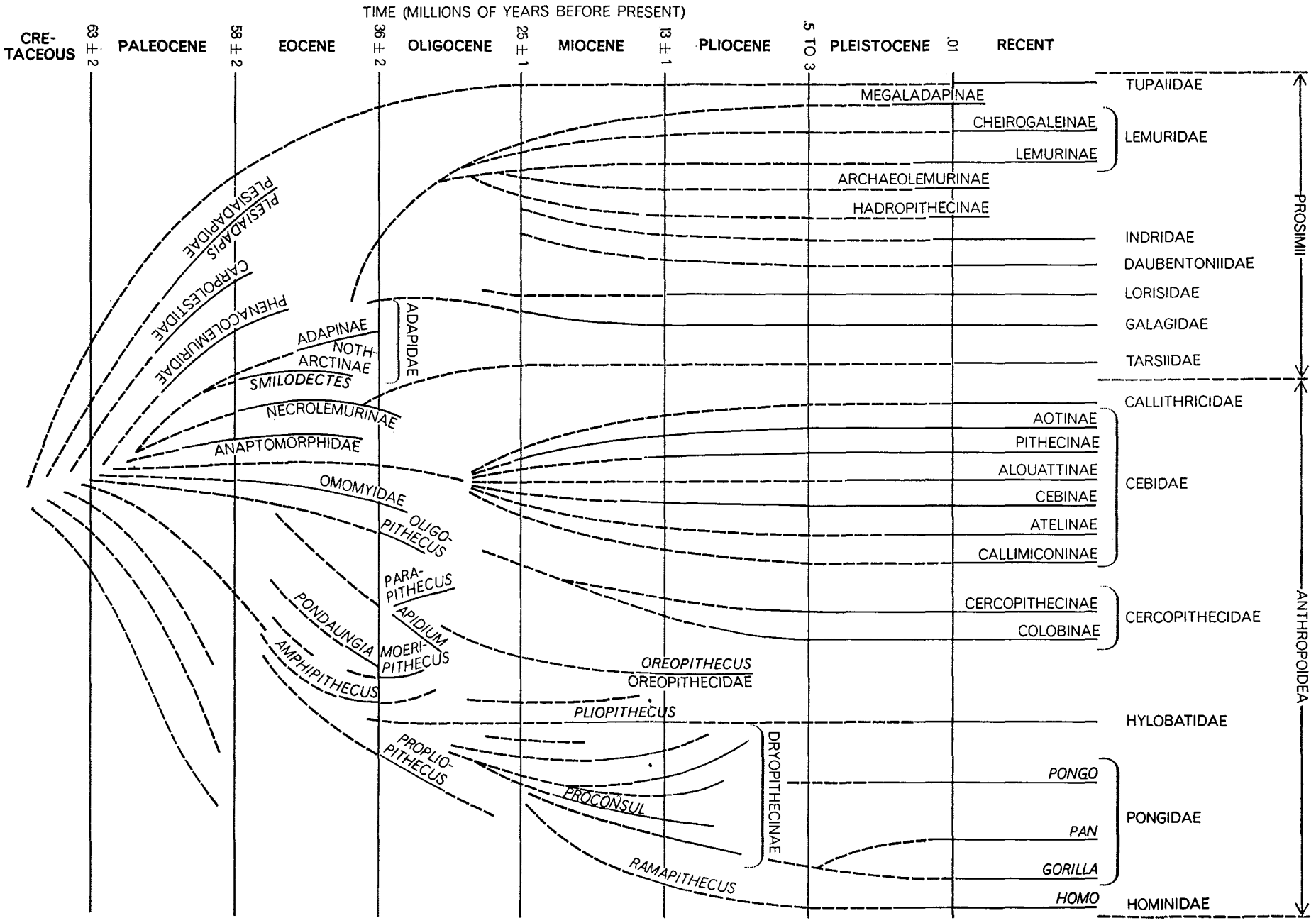
FIGURE 1



The phylogeny of the Primates (Simons, 1946).

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Pongidae—the anthropoid ape family—are grouped together in a common superfamily: Hominoidae.[21] This, of course, implies that the two families had their origin in a common ancestral stock.

There is general agreement among palaeontologists that "the divergence of the Hominidae from the Pongidae as a separate line of evolution probably dates back to the Miocene period, perhaps about 25 million years ago, and almost certainly not later than the earliest part of the Pliocene, over ten million years ago."[22] Fossil remains of a hominoid primate, termed *Dryopithecus* and dating from the Miocene and early Pliocene period, have been discovered in Europe, East Africa, India and southern China (see Figure 2). The genus *Dryopithecus* is "characterized by a dentition which is fundamentally of the pongid type, approximating quite closely to the dentition of the modern large anthropoid apes . . . ."[23] However, Le Gros Clark considers it probable that "the lineage of the Hominidae, as well as that of the modern pongids, may have stemmed from one or other of the groups of dryopithecine apes."[24]

Fossil primates dating from the early Pliocene period have been discovered in northern India and East Africa (see Figure 2) and designated *Ramapithecus* and *Kenyapithecus*, respectively. Potassium-argon dating of the *Kenyapithecus* specimen has yielded "an absolute age of about 14 million years." Both fossils are similar anatomically and are characterized by a number of physical traits "intermediate between the dryopithecines and hominids." These include the curved arc of the upper jaw of *Ramapithecus* (see Figure 3) and the "manlike ratio in comparative size of front and cheek teeth." Simons (1964) considers *Ramapithecus* "man's earliest known hominid ancestor."[25]

Early in their evolutionary history the primates adopted an arboreal habitat and became biologically adapted to this mode of life. This demanded or encouraged "prehensile functions of the limbs, a high degree of visual acuity and the accurate control and co-ordination by a well-developed brain."[26] As a consequence of the shift to an arboreal mode of life, the primate order became characterized by a number of long-run evolutionary trends.

Le Gros Clark (1971) lists ten such primate evolutionary trends, including: (1) The preservation of a generalized structure of the limbs . . . ; (2) An enhancement of the free mobility of the digits . . . ; (3) The replacement of sharp compressed claws by flattened nails . . . ; (4) The progressive abbreviation of the snout or muzzle;

[21] W. E. Le Gros Clark, *op. cit.*, p. 25.
[22] W. E. Le Gros Clark, *op. cit.*, p. 262.
[23] W. E. Le Gros Clark, *op. cit.*, p. 342.
[24] W. E. Le Gros Clark, *op. cit.*, p. 55.
[25] Elwyn L. Simons, *op. cit.*, p. 14.
[26] W. E. Le Gros Clark, *op. cit.*, p. 42.

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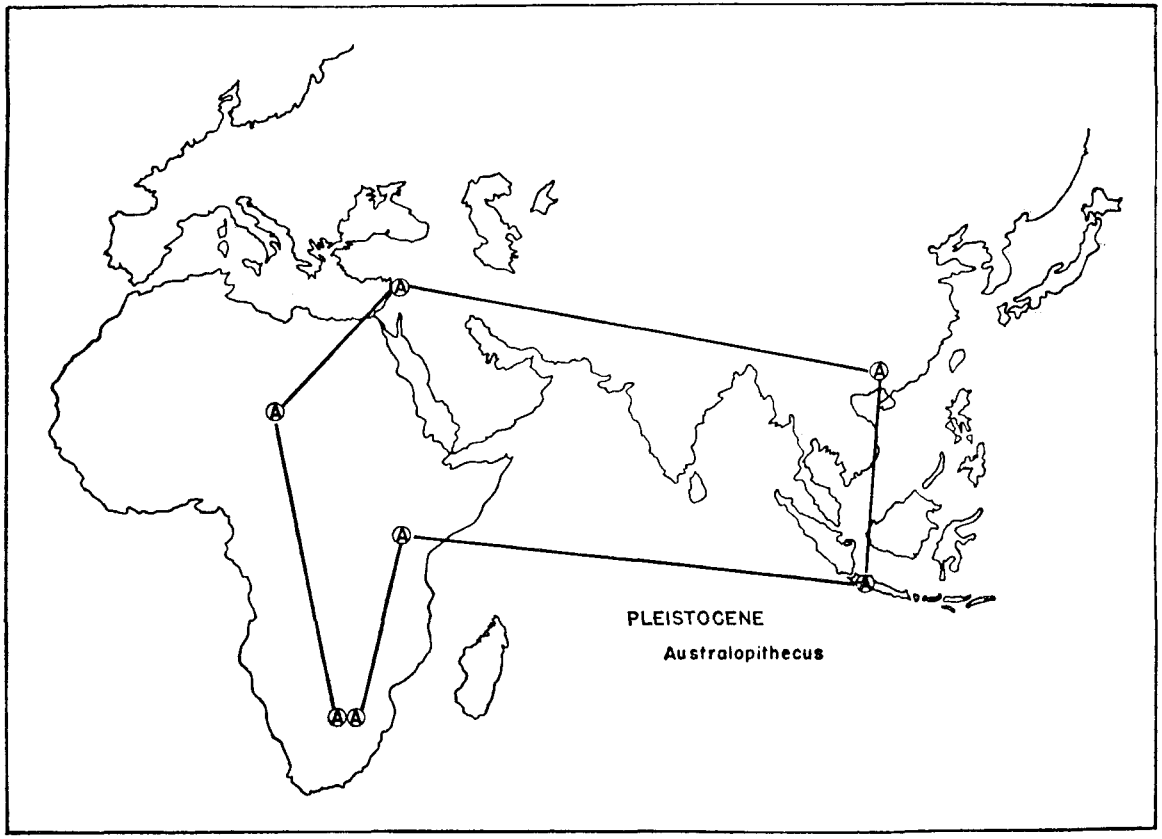
FIGURE 2



The distribution of Dryopithecine fossil finds from the Miocene and early Pliocene times (black dots). The more hominid fossil primates—*Ramapithecus* and *Kenyapithecus*—are indicated by crosses (Simons, 1964).

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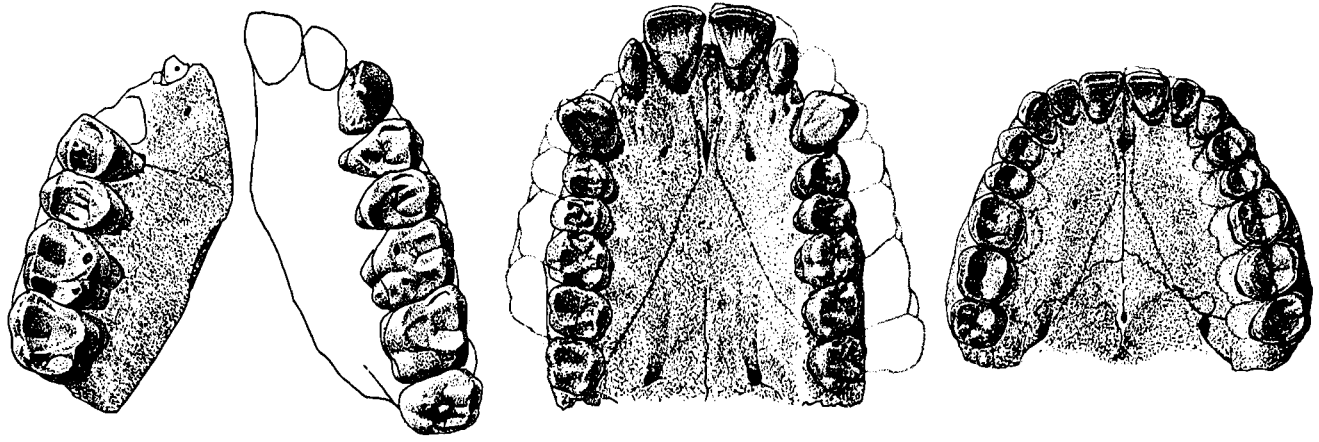
FIGURE 3



Comparison of the upper jaw of *Ramapithecus* (left), an orang-utan (center) and man (right) with the jaws drawn to the same size for comparative purposes. The curved arc of *Ramapithecus* is closer to the human shape (Simons, 1964).

(5) The elaboration and perfection of the visual apparatus with the development to varying degrees of binocular vision; (6) Reduction of the apparatus of smell; (7) The loss of certain elements of the primitive mammalian dentition and the preservation of a simple cusp pattern of the molar teeth; (8) Progressive expansion and elaboration of the brain, affecting predominantly the cerebral cortex and its dependencies; (9) Progressive and increasingly efficient development of those gestational processes concerned with the nourishment of the foetus before birth; (10) Prolongation of post-natal life periods."[27]

Le Gros Clark (1971) considers that the most distinctive trait of the primates "is the tendency towards the development of a brain which is large in proportion to the total body weight and which is particularly characterized by a relatively extensive and often richly convoluted cerebral cortex . . . ."[28] In addition to its greater relative size, the primate brain is also distinguished from that of other mammals by "certain features of its intrinsic organization."

The cerebral cortex is concerned with the reception of sensory impressions and with transforming the results into behavioral reactions. Jerison (1971) observes that "the amount and kind of nervous tissue in the brain is related to the amount and kind of sensorimotor activity that must be controlled."[29] During the evolution of the primate brain the neural apparatus of vision became highly developed. This occurred in response "to the need for a high degree of visual acuity in arboreal life." There was also associated with this "a corresponding enhancement of tactile sensibility."[30]

Le Gros Clark finds that "the olfactory cortex in the primates is thus relatively reduced in extent, while the non-olfactory areas, and particularly the visual cortex, become progressively expanded." He thus concludes that "the progressive elaboration and differentiation of the cortex in the evolving primates have led to increasing powers of apprehending the nature of external stimuli, a greater capacity for a wider range of adjustments to any environmental change, and an enhancement of the neural mechanisms for effecting more delicately co-ordinated reactions."[31]

The cortex of the primate brain is composed of a number of cortical areas, which are distinguished on the basis of structure and function. Le Gros Clark (1971) observes that the cortical areas of the primate brain undergo a progressive structural differentiation in the course of evolution, so that "their extent and boundaries become more clearly definable by histological examination."

[27] *Ibid.*

[28] W. E. Le Gros Clark, *op. cit.*, p. 227.

[29] H. J. Jerison, "More on Why Birds and Mammals have Big Brains," *The American Naturalist*, Vol. 105, No. 942, 1971, pp. 185-189.

[30] W. E. Le Gros Clark, *op. cit.*, p. 227.

[31] *Ibid.*

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This is a consequence of "the progressive refinement of the analytical functions of the cortex in the primates" and "the increasing powers of sensory discrimination served by the several cortical areas," especially the visual cortex.[32] Cyto-architectonic charts or maps have been constructed by a number of workers, on the basis of which it is possible to compare the relative extent and degree of differentiation of the various cortical areas in the brains of different primate species. Woolard (1925) constructed such a cyto-architectonic chart for the tarsier brain,[33] Bailey and von Bonin (1947) for the macaca monkey brain,[34] while Le Gros Clark (1971) presents such charts for the tree-shrew and lemur brains.[35]

Le Gros Clark (1971) also finds that "the progressive differentiation and structural contrast displayed by the cyto-architectonic areas in the higher primates are closely related to the type of convolutional pattern which characterizes their cerebral cortex." In the higher primates, many of the sulci of the brain are developed "as foldings of the cortex along the boundary lines between adjacent cortical areas (limiting sulci) or as foldings along the middle of a specific area (axial sulci)." The closer topographical relationship between the convolutional pattern and the various cortical areas is the factor "responsible for the characteristic convolutional pattern of the Anthropoidea."[36]

The expansion of the cerebral cortex in the course of evolution differentially affected the development of the lobes of the primate brain. Early in the evolution of the primates, "the occipital lobe becomes enlarged to accomodate the expanding visual cortex." Later the temporal lobe exhibits a rapid development, which "is another distinctive character of the primate brain." The temporal lobes are believed to constitute "a mechanism for the storage of visual as well as other memories." Le Gros Clark (1971) observes that there is anatomical evidence that the temporal lobes receive "impulses relayed, directly or indicrectly, from almost all other areas of the cortex" and that they appear "to provide the means for a final integration of the resultants of activity of the cortex as a whole." The frontal lobes also show a progressive expansion in the ascending scale of the Anthropoidea—*i.e.*, "from the monkeys to the apes and finally to man." The frontal lobes are believed "to form an essential part of the neural mechanism by which attention can be focused and concentrated on a particular objective."[37]

[32] W. E. Le Gros Clark, *op. cit.*, pp. 228-229.

[33] H. H. Woollard, "The Anatomy of *Tarsius spectrum*," *Proceedings of the Zoological Society of London*, 1925, pp. 1,071-1,184.

[34] Gerhardt von Bonin and P. Bailey, "The Neocortex of *Macaca mulatta*," *Illinios Monographs in Medical Science*, Vol. 5, 1947, pp. 1-163.

[35] W. E. Le Gros Clark, *op. cit.*, p. 237.

[36] W. E. Le Gros Clark, *op. cit.*, pp. 229-230.

[37] W. E. Le Gros Clark, *op. cit.*, pp. 230-231.

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TABLE 4

Primate cranial capacities
(Ashton, 1950)*

Number of crania	*Primate group*	*Mean cranial capacity*	*Standard Deviation*
34	Chimpanzee-Adult Female[1]	399 c.c.	40.6 c.c.
27	Chimpanzee-Adult Female[1]	366 c.c.	33.7 c.c.
133	Gorilla-Adult Male[2]	543 c.c.	50.0 c.c.
78	Gorilla-Adult Female[2]	461 c.c.	47.7 c.c.

* In cubic centimeters.

[1] Based on S. Zuckerman, "Age-changes in the Chimpanzee . . .," *Proceedings of the Zoological Society of London*, Vol. 98, 1928.

[2] Based on F. E. Randall, "The Skeletal and Dental Development and Variability of the Gorilla," *Human Biology*, Vol. 15, 1943.

TABLE 5

Primate cranial capacities
(Saller, 1959)*

Primate group	*Mean cranial capacity*	*Range of cranial capacity*
Hapale	6 c.c.	
Cebus	63 c.c.	48-78 c.c.
Cynocephalus (male)	163 c.c.	120-200 c.c.
Cynocephalus (female)	138 c.c.	120-160 c.c.
Macacus	103 c.c.	90-120 c.c.
Cynomolgus	60 c.c.	50-67 c.c.
Semnopithecus	65 c.c.	57-75 c.c.
Hylobates agilis	103 c.c.	81-120 c.c.
Hylobates snydactylus (male)	128 c.c.	100-150 c.c.
Hylobates syndactylus (female)	125 c.c.	105-152 c.c.
Orang-Utan (male)	395 c.c.	320-480 c.c.
Orang-Utan (female)	357 c.c.	300-390 c.c.
Gorilla (male)	508 c.c.	420-585 c.c.
Gorilla (female)	435 c.c.	370-555 c.c.
Chimpanzee (male)	404 c.c.	350-470 c.c.
Chimpanzee (female)	389 c.c.	350-440 c.c.

* In cubic centimeters.

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Although previous discussion has focused upon the evolution of the primate brain, it must be remembered that "evolution as a process concerns the whole individual or, more properly speaking, populations of individuals."[38] The various primate groups have been molded by differential selective pressures to become biologically adapted to diverse ecological niches. These evolutionary processes have brought about interrelated anatomical, physiological and behavioral changes—including changes in the structure and functioning of the brain.

Since their divergence from a common ancestral stock, "the Hominidae and Pongidae have followed very different and contrasting evolutionary trends." The anthropoid apes are "pre-eminently arboreal specialists." Their primary method of locomotion is brachiation, or "swinging with their arms." But, brachiation is associated with distinctive functional and structural adaptations, such as "a relative lengthing of the forelimb and a varying degree of atrophy of the thumb."[39]

On the other hand, the hominid ancestors of man are believed to have adopted a terrestrial or ground-dwelling mode of life. This, in turn, had far-reaching anatomical and behavioral effects. For example, once hominids "became committed to a terrestrial way of life and some degree of habitual bipedal locomotion, the freeing of their forelimbs would have greatly facilitated tool use." Pilbeam and Simons (1965) conclude that "several anatomical, behavioral and cultural elements—erect posture, orthognathism, changes in diet and display behavior, an increasing use of tools and reduction of the anterior dentition—are here closely linked one to another."[40] These anatomical and behavioral changes appear to have preceded any major structural changes in the brain—at least in so far as the parameter of cranial capacity is concerned. This, however, brings us to the next stage of hominid evolution—the Australopithecines.

THE AUSTRALOPITHECINES

In 1925 Dr Raymond Dart published a description of a juvenile fossil hominid found at Taungs in southern Africa, which he designated as *Australopithecus africanus*.[41] The fossil was that of a six or seven-year-old child, with the milk-teeth present. The face and mandible were practically complete, and "the major portion of the brain pattern can be determined from the natural endocranial cast."[42]

[38] W. E. Le Gros Clark, *op. cit.*, p. 45.

[39] W. E. Le Gros Clark, *op. cit.*, p. 48.

[40] David R. Pilbeam and E. L. Simons, "Some Problems of Hominid Classification," *American Scientist*, Vol. 53, No. 2, 1965, pp. 242-245.

[41] Raymond Dart, "*Australopithecus africanus:* the Man-Ape of South Africa," *Nature*, Vol. 115, 1925, pp. 195-199.

[42] R. Ruggles Gates, *Human Ancestry from a Genetical Point of View*, Harvard University Press, Cambridge, 1948, p. 60.

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The teeth were human-like, rather than anthropoid. The Taungs skull was found among thousands of bone fragments, indicating that *Australopithecus* was a carnivore who preyed upon baboons, antelopes, tortoises, rodents, bats and birds.[43] Broom (1933) considered that they trapped small game, "used some implement for digging, probably a sharp stone," and that they "killed the baboons with blows of a stick."[44]

Dr Dart claimed that this Australopithecine fossil was an early hominid ancestor of man. At the time, however, the majority of anthropologists and palaeontologists regarded the Taungs specimen as pongid and ancestral to the living anthropoid apes.[45] In 1936 Dr Robert Broom discovered the remains of two adults at Sterkfontein in South Africa, which he designated as *Plesianthropus Transvaalensis*. A third specimen was found in 1939 a few miles away at Kromdaai and given the generic designation of *Paranthropus robustus*.[46] The cranial capacity of all these finds was judged "to be the same as that of gorillas," while the palate showed "definite resemblances to that of man," and the dentition was "essentially human."[47]

A few years later Dr Broom found a pelvis from the fossil designated *Plesianthropus*. It was quite unlike that of a chimpanzee or gorilla. Gates (1948) concluded that "this humanoid pelvis offers final confirmation that *Plesianthropus* walked erect and was in fact in the human line of descent."[48] Subsequent studies have somewhat modified this conclusion. Contemporary authorities generally believe that "the shape of the pelvis in *Australopithecus* indicates that these hominids were habitually bipedal, although not to the degree of perfection exhibited by modern man." Napier (1967) contends that the "kind of upright walking, practiced by *Australopithecus* should not be equated with man's heel-and-toe, striding gait."[49]

Robinson (1968), in a review of Australopithecine origins, concluded that their "pelvic morphology is very closely similar to that of hominines." He noted that "erect posture is more than

[43] Raymond Dart, "A Note on the Taungs Skull," *South African Journal of Science*, Vol. 26, 1929, pp. 648-658.

[44] Robert Broom, *The Coming of Man*, Witherby, London, 1933, p. 139.

[45] Robert Broom, *op. cit.*, pp. 120-121: ". . . Little interest was taken in the discovery in England, America or Germany; and it was generally assumed that a mistake had been made by Dart, and that had he a collection of young chimpanzee skulls for comparison he would have recognized that the Taungs fossil was only the skull of a young specimen of a variety of chimpanzee."

[46] R. Ruggles Gates, *op. cit.*, p. 60.

[47] *Ibid.*

[48] R. Ruggles Gates, *op. cit.*, pp. 68-69.

[49] John Napier, "The Antiquity of Human Walking," *Scientific American*, Reprint No. 1,070, 1967, pp. 9-10.

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adequately proven by the morphology of one virtually complete pelvis with most of the spinal column and a proximal portion of femur; three other adult innominate bones and two juvenile specimens; two proximal ends of femora and two distal ends, as well as a number of skulls showing the structure and orientation of the occiput."[50]

Early estimates of Australopithecine endocranial capacities were published by Broom (1933; 1949),[51] Dart (1948),[52] and Schepers (1946).[53] Broom (1933), in a discussion of the Taungs specimen, estimated that "the adult would have a brain of about 600 c.c." If the Taungs fossil were that of a male, the adult male brain "may have had a volume of 700 c.c. or even 750 c.c."[54] Broom (1949) concluded from the dimensions of an "almost complete huge jaw" attributed to *Paranthropus crassidens* that it is improbable that in this species "the brain can have been less than 800 c.c. and very likely it may have been more than 900 c.c."[55]

Schepers (1946) estimated the range of variation of Australopithecine endocranial capacities as: from 330 to 540 c.c. for *Plesianthropus* (type 1); from 420 to 700 c.c. for *Plesianthropus* (type 2); from 490 to 815 c.c. for *Paranthropus;* and from 390 to 650 c.c. for *Australopithecus africanus*.[56] Since Broom had estimated the body weight of *Paranthropus* to be not greater than 80 or 90 lb., Schepers contended that in this Australopithecine type the ratio of brain weight to body weight exceeded that of the extant great apes. On the basis of these calculations, Schepers concluded that "in respect of brain volume, all the fossils under discussion are distinctly more advanced phylogenetically than are the living Anthropoids."[57] Dart (1948) similarly concluded that the ratio of brain weight to body weight in *Australopithecus prometheus* exceeded that of the great apes.[58] Broom and Robinson (1948), indirectly estimating the cranial capacity of the male *Plesianthropus* to be

[50] John T. Robinson, "The Origin and Adaptive Radiation of the Australopithecines," in T. D. McCown and K. A. R. Kennedy (editors), *Climbing Man's Family Tree*, Prentice-Hall, Englewood Cliffs, 1968, p. 435.

[51] Robert Broom, "Jaw of the Ape-Man *Paranthropus crassidens*," *Nature*, Vol. 163, 1949, pp. 903-905.

[52] Raymond Dart, "The Makapansgat Proto-human *Australopithecus prometheus*," *American Journal of Physical Anthropology*, Vol. 6, 1948, pp. 259-284.

[53] G. W. H. Schepers, "The Endocranial Casts of the South African Ape-Men," in R. Broom and G. W. H. Schepers, *The South African Fossil Ape-Men—the Australopithecinae*, Transvaal Museum Memoir, No. 2, 1946.

[54] Robert Broom, 1933, *op. cit.*, p. 133.

[55] Robert Broom, 1949, *op. cit.*, p. 903.

[56] G. W. H. Schepers, *op. cit.*, pp. 238-242.

[57] G. W. H. Schepers, *op. cit.*, pp. 240-241.

[58] Raymond Dart, 1948, *op. cit.*, p. 260.

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from 600 to 750 c.c., contended that "if *Plesianthropus* was not quite human, it was nearly human."[59]

Schepers (1946) also conducted a detailed analysis of the endocranial casts of five Australopithecine fossils: three *Plesianthropus Transvaalensis*, one *Paranthropus robustus* and one *Australopithecus africanus*. Dr Schepers' study comprised a description of the general morphological features of the endocranial casts, endocranial contour studies, comparative analysis of the endocranial vascular patterns, calculation of a number of brain measurements and indices, and a discussion of the neurological significance of the endocranial casts.[60]

Dr Schepers found "the vivid clarity of the convolutional pattern, particularly in the frontal region" to be a "striking feature of the endocranial casts," as compared with "the smooth casts obtained in the larger living anthropoids." In comparison with the living anthropoids, the author claimed that the Australopithecine endocranial casts showed an expansion of the frontal and parietal lobes, a reduction of the occipital lobe and an "advanced character of the temporal lobe." Schepers concluded that "the endocranial casts certainly reveal most significant evidence regarding the human affinities of these fossil types, although they are not 'advanced' in every respect, in the evolutionary sense."[61]

Dr Schepers also constructed Australopithecine cortical maps, following the system of Brodmann. He claimed that these maps showed an expansion of the primary auditory associative area (Field 21), a presence of the secondary auditory associative area (Areas 37 and 38), a large region "linked with the semantic speech function" (Area 40), a large "nominal speech area" (Area 39) and "exceptionally well developed . . . visual association centres." On the basis of these cortical maps, Schepers concluded that the Australopithecine fossil types were capable "of interpreting their immediately visible, palpable and audible environment in such detail and with such discrimination that they had the subject matter for articulate speech well under control." He also believed that they were "capable of communicating the acquired information to their families, friends and neighbours, thus establishing one of the first bonds of Man's complex social life."[62]

Since the early work of Dart, Broom and Schepers in South Africa, new discoveries and new research techniques have both added to and modified our knowledge of the Australopithecine stage of hominid evolution. These include the discoveries of

[59] Robert Broom and J. T. Robinson, "Size of the Brain in the Ape-Man *Plesianthropus*," *Nature*, Vol. 161, 1948, pp. 438-440.

[60] G. W. H. Schepers, *op. cit.*, pp. 167-272.

[61] G. W. H. Schepers, *op. cit.*, pp. 179, 181, 186, 188 and 270-271.

[62] G. W. H. Schepers, *op. cit.*, pp. 196-204 and 253.

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Australopithecine fossils in other areas of the world—beginning with L. S. B. Leakey's find in 1959 of a fossil termed *Zinjanthropus* at Olduvai Gorge in East Africa.[63] The other advances comprise new and more accurate dating techniques, revised estimates of Australopithecine endocranial capacities, re-evaluation of Australopithecine systematics, improved knowledge of the relation between behavior and biological structure and "recent observations on the behavior of free-ranging non-human primates."[64]

In 1959 Leakey reported the discovery of an adolescent Australopithecine skull from Olduvai Gorge in East Africa, which he termed *Zinjanthropus boisei*.[65] Robinson (1960), however, demonstrated that the skull and dental characters and their patterns of specialization, are "typically those of *Paranthropus*."[66] A juvenile mandible recovered by Leakey in 1961 from the bottom of Olduvai Bed I is regarded by Robinson (1968) as having "the characteristics of *Australopithecus*."[67] Other specimens of possibly middle Pleistocene age were recovered from Olduvai Bed II.[68]

Other Australopithecine finds have been reported from Java, North Africa, Palestine and South China (see Figure 4). The Javanese fossils were described by Weidenreich in 1945, who termed them *Meganthropus palaeojavanicus*.[69]

Robinson (1953; 1955), however, contends that on the basis of "the massive mandible and the combination of small canines and incisors with enormously robust postcanine teeth," *Meganthropus* is "fairly clearly a *Paranthropus*."[70] Coppens (1962) reported the discovery of an Australopithecine skull of early Villafranchian age near Lake Chad, south of the Sahara.[71] Robinson (1963) considers this specimen "closer to *Australopithecus robustus*."[72]

[63] T. D. McCown and K. A. R. Kennedy, *op. cit.*, pp. 355-359.

[64] Jane B. Lancaster, "On the Evolution of Tool-Using Behavior," *American Anthropologist*, Vol. 70, No. 1, 1968, pp. 56-66.

[65] Louis S. B. Leakey, "Facts Instead of Dogmas on Man's Origin," in T. D. McCown and K. A. R. Kennedy, *op. cit.*, pp. 388-389.

[66] John T. Robinson, "The Affinities of the New Olduvai *Australopithecine*," *Nature*, Vol. 186, 1960, pp. 456-458.

[67] John T. Robinson, 1968, *op. cit.*, p. 432.

[68] David R. Pilbeam and Elwyn L. Simons, "Some Problems of Hominid Classification," in T. D. McCown and K. A. R. Kennedy, *op. cit.*, p. 432.

[69] Franz Weidenreich, "Facts and Speculations Concerning the Origin of *Homo sapiens*," in T. D. McCown and K. A. R. Kennedy, *op. cit.*, p. 431.

[70] John T. Robinson, "*Meganthropus*, Australopithecines and hominids," *American Journal of Physical Anthropology*, Vol. 11, 1953, pp. 1-10; John T. Robinson, "Further Remarks on the Relationship Between *Meganthropus* and Australopithecines," *American Journal of Physical Anthropology*, Vol. 13, 1955, pp. 429-445.

[71] Yves Coppen, "Découverte d'un Australopitheciné dans le Villafranchien du Tchad," *Comptes-rendus Hebdomadaires des Seances de l'Academie des Sciences*. Vol. 252, No. 24, 1962, pp. 3,851-3,852.

[72] John T. Robinson, "Australopithecines, Culture and Phylogeny," *American Journal of Physical Anthropology*. Vol. 21, 1963, pp. 595-605.

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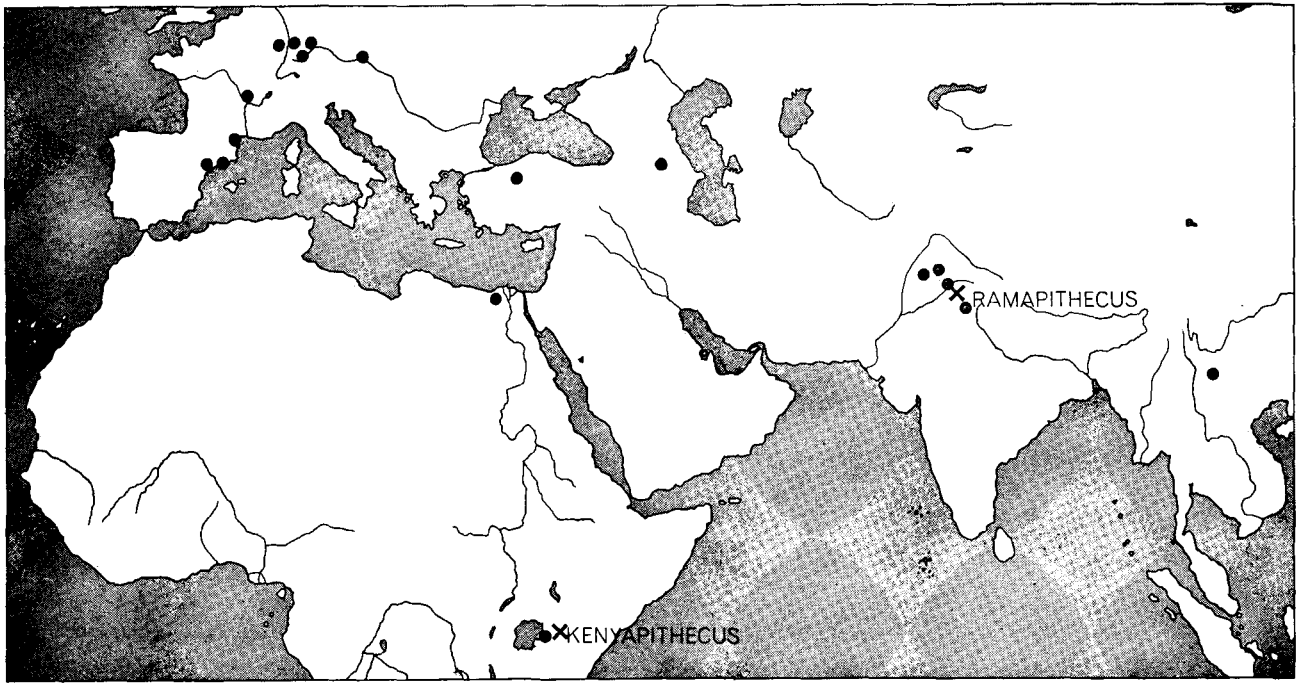
FIGURE 4



The geographical distribution of Australopithecine fossil finds (Simons, 1963).

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Australopithecine remains closer in form to *Australopithecus africanus* and of early Pleistocene age have been recovered in Ethiopia.[73] Stekelis (1960) has discovered "fragmentary hominid remains of Early or Middle Pleistocene age associated with a pebble tool culture at Ubeidiya in the Central Jordan Valley."[74] Simons (1963), in his review of hominid phylogeny, thus concludes that "if reports as to localities of *Australopithecus* by several serious students be accepted, the data now show that this earliest generally accepted antecedent of man was widely distributed in tropical regions of the Old World in the early Pleistocene."[75]

The accumulation of numerous Australopithecine fossils and fragments of fossils has permitted a more accurate determination of the cranial capacities of these early hominids. Ashton (1950) made a comparative statistical study of Australopithecine endocranial capacities and the published cranial capacity values listed for the chimpanzee, the gorilla and the later hominid *Pithecanthropus*. In this study, Dr Ashton employed the estimates of Australopithecine endocranial capacities provided by Broom, Schepers, Robinson and Dart on the basis of endocranial casts reconstructed from fragments of the crania. As a consequence "their accuracy is doubtful." The capacity of the seven Australopithecine crania employed in the study ranged from 435 c.c. to 650 c.c. with a mean of 546 c.c. (see Table 6). The mean cranial capacity of the four specimens classified as *Plesianthropus Transvaalensis* was 506 c.c.[76]

Dr Ashton (1950) compared each estimate of the cranial capacity of the Australopithecine fossils with that of the living African great apes and with Weidenreich's estimates of pithecanthropine cranial capacity by means of a simplified t-test. He found that the endocranial capacities of most of the Australopithecines "are greater than in the chimpanzee," while "none differs significantly from the male gorilla," and "all are significantly smaller than in the hominid genus *Pithecanthropus*."[77]

Carleton Coon (1962) similarly lists the estimated Australopithecine cranial capacity to range from 435 to 700 c.c.[78] He also

[73] John T. Robinson, "Further Remarks on the Relationship Between *Meganthropus* and Australopithecines," *American Journal of Physical Anthropology*, Vol. 13, No. 3, 1955, pp. 429-445.

[74] M. Stekelis, L. Picard, N. Schulman and G. Haas, "Villafranchian Deposits Near Ubeidiya in the Central Jordan Valley," *Bulletin of the Research Council of Israel*, Vol. 9-G, No. 4, 1960, pp. 175-184.

[75] Elwyn L. Simons, "Some Fallacies in the Study of Hominid Phylogeny," *Science*, Vol. 141, 1963, pp. 879-889.

[76] E. H. Ashton, "The Endocranial Capacities of the Australopithecinae," *Proceedings of the Zoological Society of London*, Vol. 120, Part IV, 1950, pp. 715-721.

[77] E. H. Ashton, *op. cit.*, p. 720.

[78] Carleton S. Coon, *op. cit.*, p. 259.

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TABLE 6

Australopithecine cranial capacities
(Ashton, 1950)*

Fossil crania	*Cranial capacity*
Plesianthropus transvaalensis 1	435 c.c.
Plesianthropus transvaalensis 2	560 c.c.
Plesianthropus transvaalensis 3	500 c.c.
Plesianthropus transvaalensis 4	530 c.c.
Paranthropus robustus	650 c.c.
Australopithecus africanus	500 c.c.
Australopithecus prometheus	650 c.c.
Mean cranial capacity (7 Crania)	546 c.c.

* In cubic centimeters.

TABLE 7

Revised Australopithecine cranial capacities
(Holloway, 1970)

Fossil crania	*Cranial capacity*
1. Taung	440 c.c.
2. Sts 60	428 c.c.
3. Sts 5	485 c.c.
4. Sts 19	436 c.c.
5. Sts 71	428 c.c.
6. MLD 37/38	435 c.c.
7. "Zinj"	530 c.c.
8. SK 1585	530 c.c.
Mean cranial capacity	464 c.c.
Standard deviation	45 c.c.

notes that estimates of the body weight of the Australopithecines have been made, "based principally on pelvis size." One group of these early hominids is believed to be under five feet in height and to weigh less than 100 lb. The Australopithecines from Swartkrans and Kromdaai in South Africa appear to be taller and heavier, possibly weighing as much as 150 lb.[79] Dr Coon thereby concludes that "the brains of both putative species of Australopithecines were a little larger for their body size than the brains of the three living great apes, but not enough larger to indicate, without supplementary evidence, a substantial difference in intelligence."[80]

[79] Carleton S. Coon, *op. cit.*, p. 235.
[80] Carleton S. Coon, *op. cit.*, p. 259.

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The questioning of the accuracy of some of the early estimates of Australopithecine endocranial capacities led Dr Ralph Holloway of Columbia University to conduct a special study of their endocranial remains. He made complete reconstructions of eight Australopithecine fossil crania. The cranial volumes "were determined by the average of five water displacement measurements, multiplying the average by two to obtain total volume." Dr Holloway's newly determined Australopithecine endocranial values are presented in Table 7, where they are compared with the previous values listed in the anthropological literature. As can be seen from the table, the new mean cranial capacity of 464.00 c.c. is some seven per cent less than the previously listed Australopithecine mean of 497.14 c.c.[81]

By way of comparison, Ashton (1950) reports the mean cranial capacity in a series of 34 adult male chimpanzees to be 399 c.c. (see Table 4).[82] Saller (1959) lists the mean cranial capacity of the male chimpanzee at 404 c.c., with a range of 350 to 470 c.c. (see Table 5).[83] The body weight of the chimpanzee is approximately the same as the estimates calculated for the smaller Australopithecines—80 to 90 lb. for the adult female and 100 to 110 lb. for the adult male chimpanzee. Consequently, it would appear that this early hominid represents an evolutionary stage with behavioral capacities little advanced over those of the higher primates—especially the chimpanzee. The finding by Holloway of an even lower mean cranial capacity for an Australopithecine series than previously reported in the anthropological literature, lends further support to the view of Dr Grover Krantz that "*Australopithecus africanus* is an earlier ancestor which did not depend on cultural behavior any more than do recent anthropoid apes."[84]

Most contemporary anthropologists doubt that the Australopithecines possessed "true speech." Gates (1948), for example, suggests that "there was probably no speech then, but only cries, gestures and facial expressions, the features being much more refined than in the apes."[85] Von Eickstedt (1959), noting that no *Spinae mandibulae* have been observed on the inner border of the symphysis of the lower jaw, concluded that the Australopithecines possessed "no true speech" ("*keine eigentliche Sprache*").[86] Coon

[81] Ralph L. Holloway, "New Endocranial Values for the Australopithecines," *Nature*, Vol. 227, No. 5,254, 1970, pp. 199-200.

[82] E. H. Ashton, *op. cit.*, p. 716.

[83] Karl Saller, *Lehrbuch der Anthropologie*, Gustav Fischer, Stuttgart, Germany, Vol. II, 1959, p. 1,220.

[84] Grover Kratz, *The Origin of Man*, Dissertation Abstracts International, Vol. XXXII, No. 5, 1971.

[85] R. Ruggles Gates, *op. cit.*, p. 62.

[86] Egon von Eickstedt, *op. cit.*, pp. 1,215-1,216.

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(1962), in his review of Australopithecine phylogeny, also contends that "it is extremely unlikely that they could speak."[87]

Schepers' interpretation of the neurological significance of the Australopithecine endocranial casts has been criticized by later workers. Weidenreich (1947), in his review of Schepers' work, contended that ". . . it is absolutely impossible to read any neural functions, such as described by Schepers, from the impressions that the convolutions of the brain leave on the walls of the cranial cavity . . . ." Hence, "there is not the slightest justification for such far-reaching conclusions as drawn by Schepers."[88]

The Russian anatomist, V. I. Kotchetkova (1960), has conducted a more recent comparative study of the endocranial casts of fossil and living men. With respect to the Australopithecines, Dr Kotchetkova observed that ". . . the macrostructure of the brain comes near that of the present-day monkey." He also contended that "the characteristic fusion of the temporal and frontal regions, as well as the macrostructure of the inferior frontal part of the Australopithecine endocranial cast, leads to the conclusion that *Australopithecus africanus* did not possess articulate language."[89]

The new method of dating that has recently become available is potassium-argon dating, which is based on the rate of decay of radioactive potassium into argon. This method provides an absolute date for the object tested in contrast to the older method of relative dating derived from sequences of geological strata.[90]

The advent of potassium-argon dating has greatly altered estimates of the dates and duration of the early part of the Pleistocene period. In 1959 Zeuner estimated the duration of the Pleistocene to be one million years.[91] The minimal estimate for the start of the Pleistocene is now two million years ago, with a possibility of the Pliocene-Pleistocene boundary being more than three or four million years ago (see Table 8). The earliest part of the Pleistocene, the Villafranchian, "is now seen as lasting 2.5 million years and comprising three-quarters of the total length of the Pleistocene." This revised estimate of the Pleistocene time span has in turn altered views of "the rate of development of tool-using abilities and techniques" and of "the interrelation of tool types to the biology of their makers."[92]

[87] Carleton S. Coon, *op. cit.*, p. 259.

[88] Franz Weidenreich, *op. cit.*, p. 349.

[89] V. I. Kotchetkova, "L'évolution des regions specifiquement humaines de l'écorce cérébrale chez les Hominides." *Proceedings Sixth International Congress of Anthropological and Ethnological Sciences*, Paris, Vol. 1, 1960, pp. 623-630.

[90] Jane B. Lancaster, *op. cit.*, pp. 56-68.

[91] F. Zeuner, *The Pleistocene Period: Its Climate Chronology and Faunal Successions*, Hutchinson, London, 1959.

[92] Jane B. Lancaster, *op. cit.*, pp. 56-57.

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TABLE 8

Chronology of the Pleistocene
(Lancaster, 1968)

	Geological period	*Radiometric age estimates*	*Tool tradition*
Upper Pleistocene	Third interglacial (Eemian)	100,000 B.P.	
Middle Pleistocene	Second interglacial (Holstein)	255,000 B.P. or more	
	First interglacial (Cromerian)	700,000-500,000 B.P.	Acheulian and later traditions
		1,000,000 B.P.	
Lower Pleistocene	Villafranchian	2,000,000 B.P.	Oldowan tools
	(Early Villafranchian?)	3,000,000-2,500,000 B.P.??	

From the standpoint of evolutionary development, "behavior and structure form an interacting complex, with each change in one affecting the other." Washburn (1960), noting that stone tools had been found in association with Australopithecine remains more than 500,000 years old, contended that "the structure of modern man must be the result of the change in the terms of natural selection that came with the tool-using way of life." The pelvis of the Australopithecines "corresponds closely, though not precisely, to that of modern man," so that "the adaptation to bipedal locomotion is not yet complete" at this stage of evolution.[93]

Washburn (1960), therefore, believed that "tool use is both the cause and the effect of bipedal locomotion." That is, "the advantage that these objects gave to their users led both to more bipedalism and to more efficient tool use." In the process of natural selection cause and effect are interrelated with selection being based "on successful behavior." Hence, Washburn concluded that "the success of the new way of life based on the use of tools changed the selection pressures on many parts of the body, notably the teeth, hands and brain, as well as on the pelvis."[94]

The model of an accelerating pace of evolution due to the adaptive advantages of tool-use in which "advances were assumed to have come in rapid succession as the brain, tool-making techniques and cultural traditions interacted in a mutually stimulating feedback relationship" is not supported by recent scientific

[93] S. L. Washburn, "Tools and Human Evolution," *Scientific American*, Reprint No. 601, 1960, pp. 3-7.

[94] S. L. Washburn, *op. cit.*, pp. 3-15.

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TABLE 9

Chronology of the evolution of tool-using behavior
(Lancaster, 1968)

Geological time divisions	*Radiometric age estimates*	*Tool-using species of primates*	*Types of tool-using traditions*
Pleistocene	700,000-500,000 B.P.	*Homo erectus* (one species only)	Hand axe and later traditions
	2,000,000 B.P.	*Australopithecus* (more than one species)	Oldowan industries
Pliocene	13,000,000 B.P.	Pongid and Hominid (many species)	Unskilled, ape tool use (hypothetical)

observations and discoveries. At Olduvai Gorge in East Africa, chopping tools, polyhedral "flaked" stones and other utilized stones have been found in layers dated between 1.9 and 1.75 million years ago. These same stratigraphic layers have also yielded the fossil remains of two small-brained Australopithecine individuals.[95]

Lancaster (1968) observes that "the elementary stone techniques and poorly standardized tool-making tradition of the Oldowan appears in East Africa to have lasted at least one million years and quite probably for more than double that time with little change or advance in their manufacture or in the biology of their makers." This means that the Oldowan tool tradition is now assigned a time span of 2,000,000 B.P. to 500,000 B.P., or possibly 2,500,000 B.P. to 500,000 B.P. (see Table 9). The makers of these tools are the relatively small-brained Australopithecines. Hence, Dr Lancaster concludes that "the early part of the evolution of stone tools and of man must have proceeded at a rate very different from the later stages and advances must have come very much more slowly."[96]

Pilbeam and Simons (1965) similarly note that "the primitive stone tools associated with *Homo habilis* throughout Bed I and the lower part of Bed II are evidently of uniform type for what may be a very long period of time; this is perhaps correlated with the equally protracted apparent stability of cranial capacity . . . ."[97] Consequently, the authors conclude that "dates from Olduvai suggest the possibility that a full million years passed after the invention and spread of tool-making during which cranial capacity—and presumably manual dexterity, "intelligence," and hunting skill—remained fairly constant."[98]

[95] Jane B. Lancaster, *op. cit.*, pp. 56-57.

[96] *Ibid.*

[97] David R. Pilbeam and Elwyn R. Simons, *op. cit.*, p. 415.

[98] *Ibid.*

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Furthermore, it now appears that tool-use is not unique to man. Dr Jane Goodall (1964) has found that "tool-use in the chimpanzee is an important behavior pattern." Chimpanzees use tools both for obtaining food and for defense. Food is obtained by using twigs and grass blades for "fishing" ants or termites out of their nests. Rocks and sticks are aimed and thrown at man and other animals by chimpanzees as part of a sequence of aggressive display.[99] By human standards, however, tool-using behavior in chimpanzees appears clumsy and is ambidextrous. Lancaster (1968) interprets these characteristics as possibly "indicative of the limitations that the chimpanzee's brain places on its ability to develop highly skilled tool use.[100]

The picture of the evolution of tool-using behavior that can be drawn from this research can be summarized as follows. A kind of unskilled ape tool use emerged during the early part of the Pliocene period, "continued without major changes for millions of years and has continued down to the present in one or more of the surviving descendant species of ape." The onset of the Pleistocene period saw the emergence of the relatively small-brained bipedal hominids, known as *Australopithecus*, which relied upon tool-use for much of their food-getting and defense. The importance of tools to their way of life is indicated by "specializations in the hand and especially the thumb, the reduction in the canines and incisors and bipedalism." The Australopithecines "lasted without major changes in either anatomy or tool traditions for a long time, perhaps 2.5 million years."[101]

The taxonomic status of the Australopithecines has also been modified and revised since the early discoveries of Dart and Broom. Coon (1962),[102] Mayr (1963),[103] Leakey (1965),[104] Pilbeam and Simons (1965), [105] Robinson (1968),[106] and Le Gros Clark (1971)[107] have treated Australopithecine taxonomy in their reviews of hominid phylogeny. In a 1950 article, Dr Robert Broom grouped the South African Australopithecines alone into five species of three genera, with the Makapan form being a possible fourth genus.[108] Most

[99] Jane Goodall, "Tool-Using and Aimed Throwing in a Community of Free-living Chimpanzees," *Nature*, Vol. 201, 1964, pp. 1,264-1,266.

[100] Jane B. Lancaster, *op. cit.*, p. 59.

[101] Jane B. Lancaster, *op. cit.*, pp. 63-64.

[102] Carleton S. Coon, *op. cit.*

[103] Ernst Mayr, "The Taxonomic Evaluation of Fossil Hominids," in T. D. McCown and K. A. R. Kennedy, *op. cit.*, pp. 372-386.

[104] Louis S. B. Leakey, *op. cit.*, pp. 387-409.

[105] David R. Pilbeam and Elwyn R. Simons, *op. cit.*, pp. 410-431.

[106] John T. Robinson, 1968, *op. cit.*, pp. 432-448.

[107] W. E. Le Gros Clark, *op. cit.*

[108] Robert Broom, "The Genera and Species of the South African Fossil Ape-Man," *American Journal of Physical Anthropology*, Vol. 8, 1950, pp. 1-13.

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contemporary writers recognize only two hominid genera—*Australopithecus* and *Homo*. Le Gros Clark (1971), for example, considers that *Australopithecus* is "properly to be classed as a genus of the Hominidae," since "the morphological details of the dentition, and the structural adaptations in the pelvis and other parts of the skeleton for an erect posture and gait, make it clear that the genus had already advanced a considerable distance along the evolutionary trends distinctive of the Hominidae."[109]

Two types of Australopithecines are currently recognized—a "gracile" (*Australopithecus africanus*) and a "robust" (*Paranthropus robustus*).[110] These are regarded by some writers as representing "two seperate species of the genus." Robinson (1968) distinguishes the two forms on the basis of differences in dental and skull morphology (see Figures 5 and 6).[111] Other differences have been observed in "the nature and shape of the palate, the shape and structure of the face and of the braincase."[112] Robinson also finds that "*Paranthropus* is known from South Africa, East Africa and Java," while "*Australopithecus* is known from both South Africa and East Africa, but not from the Far East—on currently available evidence."[113]

Anthropologists differ, however, in their views regarding the extent to which the various Australopithecines are ancestral to later hominids. Carleton Coon (1962), for example, notes the close similarity of the bones and teeth of *Australopithecus* and *Homo* and concludes that "some kind of close genetic continuity between them must be accepted." He then poses the question: "Did the known Australopithecines, having undergone an evolutionary sequence of their own, simply become men at the end of the Lower Pleistocene after they had begun to hunt, to speak and to sit around fires; or did some early kind of Australopithecine like Sterkfontein or the Olduvai child evolve into *Homo* while *Swartkrans* and *Zinjanthropus* pursued their own genetic blind alleys to extinction?"[114]

Mayr (1963) also observes that "*Homo* passed through an *Australopithecus* stage," even though "*Homo* and *Australopithecus* have been found to be contemporaries." He concludes that "the Australopithecines consisted of several species" and that "only a segment of this assemblage gave rise to *Homo*." Hence, much of the remainder must have "persisted contemporaneously with *Homo*, without rising above the Australopithecine grade."[115]

[109] W. E. Le Gros Clark, *op. cit.*, p. 48.

[110] Laura Evans, "Ancestral Secrets," *The Sciences*, Vol. 12, No. 3, 1972, pp. 16-22.

[111] John T. Robinson, 1968, *op. cit.*, pp. 422-431.

[112] John T. Robinson, *op. cit.*, p. 425.

[113] John T. Robinson, *op. cit.*, p. 433.

[114] Carleton S. Coon, *op. cit.*, p. 302.

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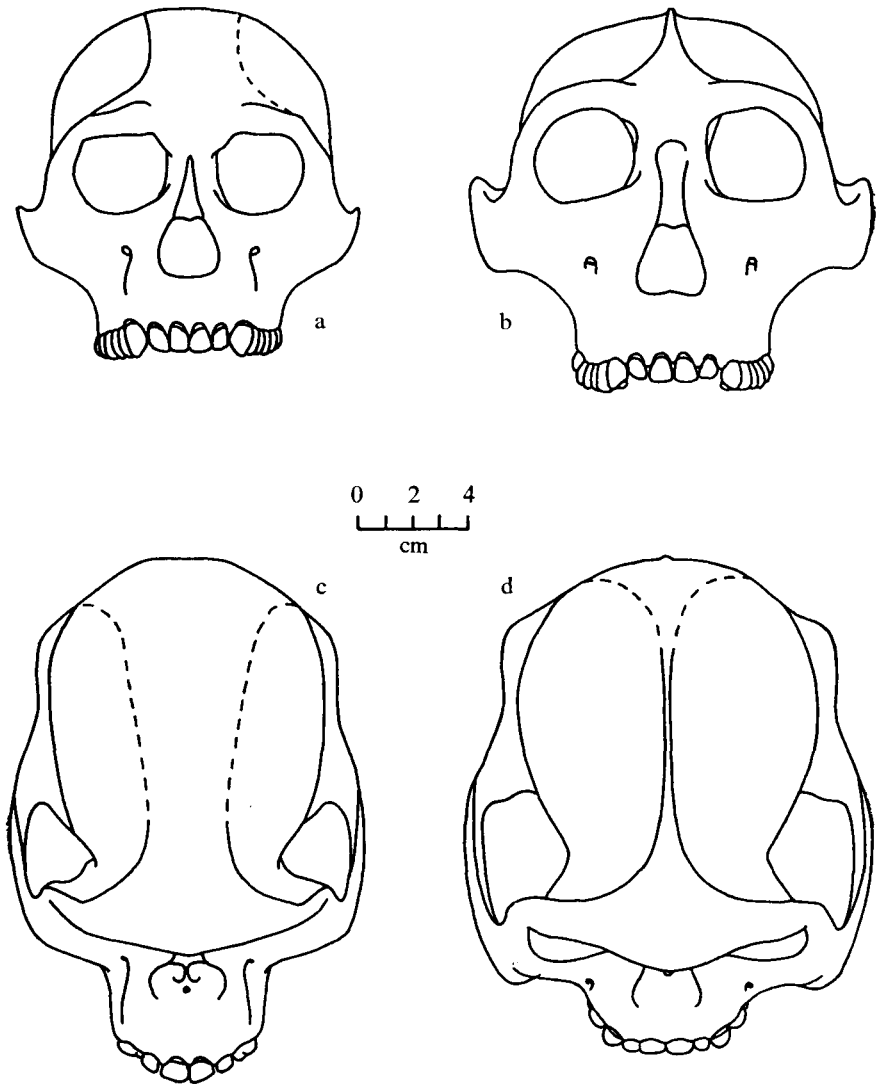
FIGURE 5



Facial views of female skulls of (a) *Australopithecus* and (b) *Paranthropus;* top views of female skulls of (c) *Australopithecus* and (d) *Paranthropus* (Robinson, 1968).

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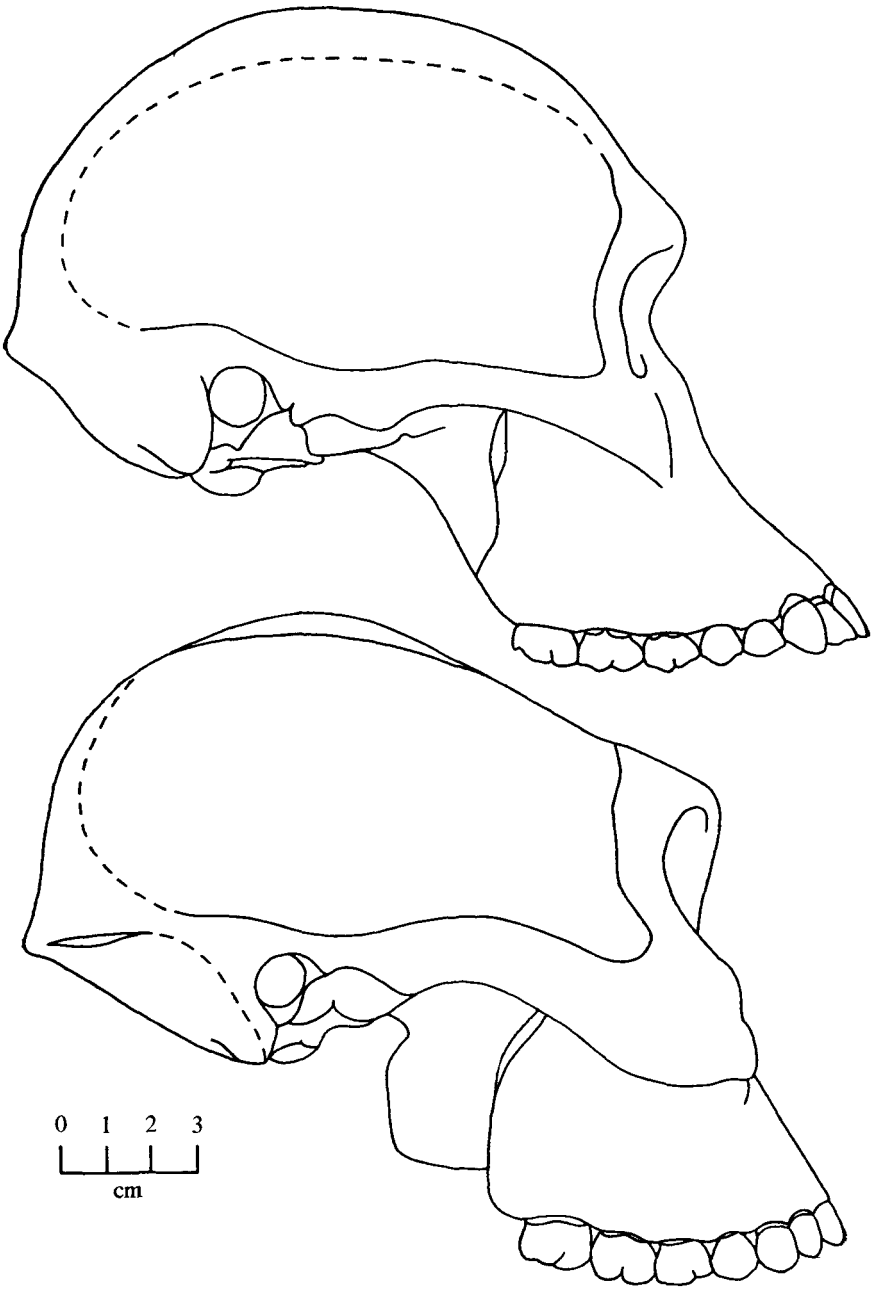
FIGURE 6



Side views of female skulls of *Australopithecus* (upper) and *Paranthropus* (Robinson, 1968).

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Leakey (1965) finds that *Australopithecus* (*Zinjanthropus*) is present in the early part of Olduvai Bed I and "runs right up the series to the higher part of Bed II." A second type of hominid, which Leakey terms *Homo habilis*, is found at the bottom of Olduvai Bed I and continues up in a level of Olduvai Bed II "which in other parts of the Gorge are yielding hand axes." A third type of hominid, found in the upper part of Bed II, is regarded by Leakey as "morphologically Pithecanthropine"—though "it is certainly not Pithecanthropine in the Java or Pekin sense." Consequently, Dr Leakey concludes that at Olduvai "there are three contemporaneous, co-existent hominids in the upper part of Bed II, the *habilis* type, the *Pithecanthropus* type, and, still continuing, an *Australopithecus* type."[116]

Robinson (1968) presents an extensive discussion of "The Origin and Adaptive Radiation of the Australopithecines." He regards Leakey's taxonomic designation of *Homo habilis* "as invalid as a new species of hominid." He finds the Olduvai Bed I material "to be very similar to South African material of *Australopithecus* (senus stricto) in its morphology."[117] However, Dr Robinson contends that the two Australopithecine forms—*Paranthropus* and *Australopithecus*—"were not only different in morphology but also in behavior and ecology and that *Paranthropus* represents a stable adaptation."[118]

According to Robinson, *Paranthropus* was vegetarian and "represents basically the original Australopithecine stock." On the other hand, *Australopithecus* "represents an adaptively different line evolving in a different direction."[119] Dr Robinson suggests that "the changed environmental circumstances resulting from the known desiccation of a substantial part of Africa during the later Tertiary could therefore very easily have led to a second adaptive shift and the establishment of a second phyletic line in the Australopithecines in which carnivorousness and an enhanced level of cultural activity were important features."[120] This line is *Australopithecus*.

Robinson even contends that "the adaptive shift occasioned by increasing aridity and the necessity to use meat as a normal part of the diet was a second critical point in the evolution of hominines"—*i.e.*, with the first being the adaptive shift to erect posture. Meat eating is thus viewed as "placing a heavy premium on tool-using and improved intelligence," whose natural consequence was "the

[115] Ernst Mayr, 1963, *op. cit.*, p. 378.
[116] Louis S. B. Leakey, *op. cit.*, p. 393-394.
[117] John T. Robinson, *op. cit.*, pp. 445-446.
[118] John T. Robinson, *op. cit.*, p. 448.
[119] John T. Robinson, *op. cit.*, p. 440.
[120] John T. Robinson, *op. cit.*, p. 441.

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development of the hominine grade of organisation."[121] Dr Robinson also believes that "the hominine brain expansion had already started in *Australopithecus*, as is indicated by the relatively high-domed brain case . . . , whereas in *Paranthropus* this had not begun."[122] He interprets Leakey's Olduvai material as representing an *Australopithecus* lineage which "was changing steadily through all of the time during which the *Paranthropus* line appears to have been stable."[123] Elsewhere—at Swartkrans and Sangiran—*Paranthropus* appears to be contemporaneous with early forms of *Homo erectus*.

On the basis of current knowledge, we may conclude that the Australopithecine stage of evolution persisted for a considerable period of time—from the beginning of the Lower Pleistocene to the Middle Pleistocene. This extends in absolute terms from at least 2,500,000 years before the present—and possibly three or even four million years B.P.—to some 500,000 years B.P. Analysis of both the fossil remains and the cultural evidence indicates an extremely slow pace of evolution. The Australopithecines were characterized by a simple pebble-tool culture—termed the Oldowan tradition. The mean cranial capacity of the Australopithecines is in the range of 450 to 550 c.c., which is little advanced over that of the chimpanzee. Cranial capacity remained constant in this range throughout the Lower Pleistocene. It appears unlikely that the Australopithecines possessed true speech. However, the Australopithecines differ from the pongids in having a nearly erect bipedal posture, a primitive culture and a hominid-like dentition. The change to erect bipedal posture and locomotion represented a major adaptive shift which freed the hands for effective tool-use. This was an important step toward hominization. The Australopithecines have been classified into at least two species and are found distributed throughout the tropical regions of the Old World. Some of these Australopithecines are found contemporaneous with early *Homo* in the early Middle Pleistocene. This, however, brings us to the next stage of hominid evolution—the Pithecanthropine or *Homo erectus*.

APPENDIX

The discovery by Richard Leakey near Lake Rudolf in East Africa of two intact thighbones and cranial fragments which have been assembled into a skull may further revise our views of the origin and evolution of man. According to newspaper accounts (*New York Times*, 10th November 1972), the new fossils were discovered in sand strata "below volcanic deposits which have been accurately dated at 2,600,000 years." The skull had been crushed

[121] John T. Robinson, *op. cit.*, p. 443.
[122] John T. Robinson, *op. cit.*, p. 446.
[123] John T. Robinson, *op. cit.*, p. 448.

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to hundreds of fragments which were pieced together by Dr Leakey and his wife.

Dr Leakey's reconstruction is that of a skull "lacking the heavy and protruding eyebrow ridges and thick bone that are characteristic of *Homo erectus* known from young deposits in both Africa and Asia." Dr Leakey claims that the new fossil is "definitely of the genus *Homo*, though different from *Homo erectus* and from *Homo sapiens* of today" (*The National Observer*, 18th November 1972). He estimates the cranial capacity to be about 800 c.c. This is almost intermediate between the mean Australopithecine cranial capacity of less than 500c.c. and the mean Pithecanthropine or *Homo erectus* cranial capacity of more than 1,000 c.c.

If the dating, cranial reconstruction, and cranial capacity estimate are correct, this would indicate a more advanced hominid contemporaneous with *Australopithecus* at a much earlier date than previously believed. Should Dr Leakey's discovery and interpretation be confirmed by additional fossil finds, it would appear that the Australopithecines played less of a rôle in the origin and evolution of modern man than previously estimated. It is possible that Leakey's find and the contemporaneous Australopithecines were both derived from the earlier Australopithecines of some four million years of age, or that both groups evolved from an earlier common ancestor as yet undiscovered. However, such far-reaching reconstructions of hominid phylogeny have to await further work in this field.

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